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), sawflies (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-

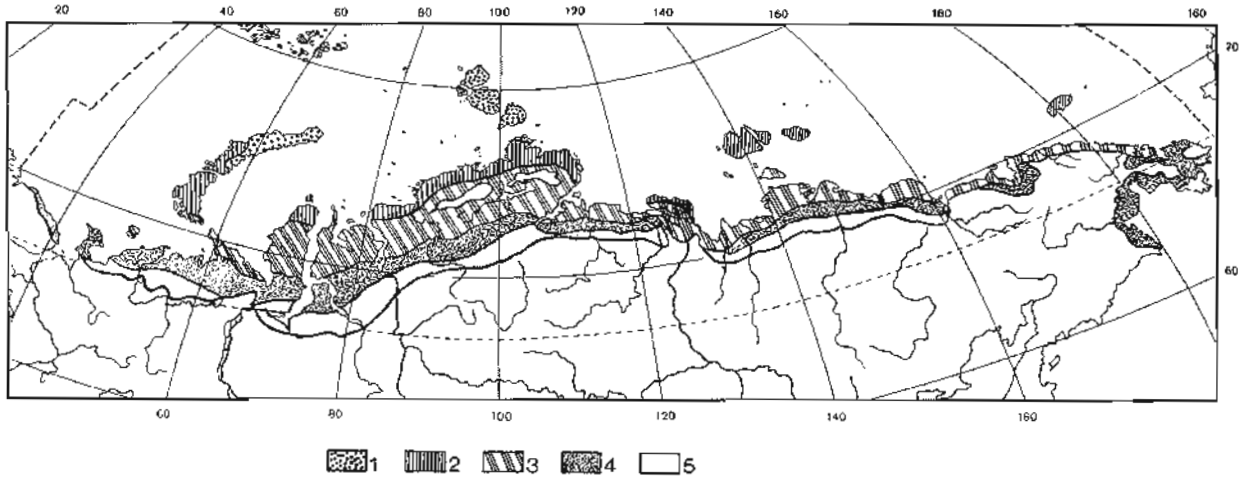


Fig. 16.1. The basic zonal landscapes of the Eurasian Arctic. 1, polar desert; 2, arctic tundra subzone; 3, typical tundra subzone; 4, southern (shrub and tussock) tundra subzone; 5, southern limit of the forest tundra.

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

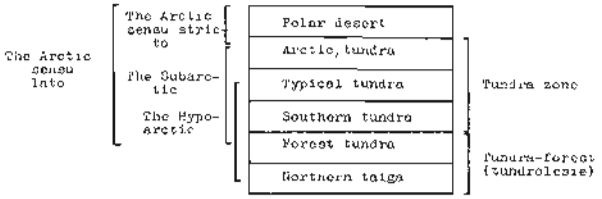


Fig. 16.2. Latitudinal zonation of the Arctic. Modified from Chernov and Matveyeva (1979).

has been developed, which practically disappears in the Kola peninsula. East of Taymyr, the lowland tundra also extends along the coast as a narrow belt. Its northern variant is represented there mainly on the islands (Novosibirskiye Islands and Vrangel Island). Forest tundra extends in a narrow belt with a width of 30–150 km, disappearing towards the east on the mainland.

The entire treeless territory around the North Pole is often called the "Arctic". In a narrow sense, as used by specialists, this means the basin of the Arctic Ocean and its ice-covered islands, the polar desert, and the variant of the tundra occurring at the highest latitudes. In Russia, the territory situated further south, where the tundra landscape has mainly developed, is often called the "Subarctic" (Grigor'ev, 1956, 1970). As a territory, the Subarctic thus defined does not fully coincide in extent with the tundra zone; to the north, it does not reach as far as the tundra and in the south, it includes the forest tundra. In this context, the Subarctic can be understood to be the same as the "Low-Arctic" – that is, a part of the Arctic. By "Subarctic", non-Russian authors often mean areas which can definitely be considered as "south of the Arctic" in the broad sense of the term.

Another category of latitudinal division of polar areas has been used in Russia, namely the "Hypoarctic", which includes the southern half of the tundra zone, the forest tundra, and part of the northern taiga (Yurtsev, 1966).

In recent times, some Russian explorers investigating the northeastern biomes of the country began to use the concept of tundra forest ("tundrolesie"), meaning territories with depressed and sparse forest vegetation and with combinations of forest and tundra ecosystem components (Parmusin, 1979).

The application of some terms for the latitudinal division of polar areas commonly used in Russian literature is given in Figure 16.2. "Arctic" and "Subarctic" correspond with concepts of the geographical environment, whereas "tundra zone", "polar desert", and "forest tundra" have landscape and cenotic meanings, and "Hypoarctic" is a biogeographical category.

The zonal division of the northern Eurasian areas and the islands of the Arctic Ocean shown in Figure 16.2 is not the only one existing in Russian literature. Some authors do not recognize polar desert as a separate zone and consider it as a subzone of the tundra zone (Yurtsev et al., 1978). In our opinion, polar desert must be distinguished as a special natural zone. It is characterized not only by scarcity of life, but also by many special features in the landscape and community structure, in species composition, and in the food relations between animals and plants (Matveyeva and Chernov, 1976; Aleksandrova, 1977, 1983; Chernov et al., 1979; Matveyeva, 1979b).

On the other hand, many authors consider forest tundra a zone; but it cannot be divided into distinct latitudinal parts. However, in respect of its area, the type of vegetation and soil cover is hardly comparable to either the tundra or the forest zone. It could actually be regarded as a transition belt between the tundra and the taiga or as a zone of secondary order (Chernov, 1975). Thus, the two types of forest zones, the taiga and the deciduous forest, are separated in the north by the forest tundra from another pair of zones, the tundra and the polar desert.

The tundra zone can be divided into three subzones: arctic, typical, and southern. Such division of the tundra zone was proposed in Russian literature as early as the 1930s (Sambuk and Dedov, 1934; Gorodkov, 1935). In spite of some attempts to change this system (Aleksandrova, 1971; Yurtsev et al., 1978), we consider it the most rational, although we do not reject the other approaches to the zonal–latitudinal differentiation. In the present paper, we have used the following latitudinal divisions of polar areas within Russia: polar desert zone, tundra zone including arctic, typical, and southern subzones, and the forest tundra transition belt.

The areas occupied by variants of zonal landscapes differ greatly in size. Thus, the arctic as well as the southern tundra subzones are much narrower than the typical tundra. Especially small is the area of polar desert. Polar desert occupies about 100,000 km^2 in Eurasia; the area of the arctic tundra is no more than 200,000 km^2; and that of the typical tundra is about 400,000 km^2. It

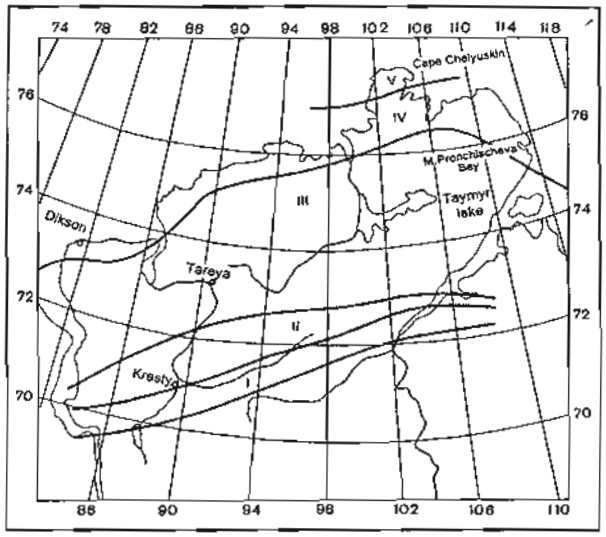


Fig. 16.3. Taymyr Peninsula subdivisions in zones and subzones. Thick lines show the borders of the tundra zone. I, forest tundra; II, southern tundra; III, typical tundra; IV, arctic tundra; V, polar desert. From Chernov and Matveyeva (1979).

is very difficult to estimate accurately the area of the southern tundra because the limits of this subzone in western Siberia and in northeastern Asia are still unknown.

The tundra and the polar desert are not equally represented in the whole Eurasian continent. For example, only southern tundra occurs on the Kola peninsula, while only southern and typical tundras are found in northern Europe and only arctic tundras and polar deserts in Novaya Zemlya. In northern Siberia, southern and typical tundras are very well developed in the vast area, whereas in Chukotka, which is mostly occupied by mountains, the plain tundra is represented mainly by its southern variants.

All three tundra subzones as well as the polar desert are well represented in only one extensive mainland territory (not only in Eurasia, but on the whole globe) – namely, the Taymyr peninsula in the extreme north of Siberia (Fig. 16.3).

TABLE 16.1 *

Annual and total summer radiation in the eastern European tundra zone

Observation area	Total annual solar radiation (kcal cm^{-2} yr^{-1})	Total solar radiation	
		April–September (kcal cm^{-2} (%))	June–August (kcal cm^{-2} (%))
Northern part of tundra zone	64	58 (91)	35 (55)
Southern part of tundra zone	70	61 (87)	36 (51)

From Grigor'ev (1956).

CLIMATIC CONDITIONS

Solar radiation

Total solar radiation in the tundra regions of Eurasia amounts to around 70 kcal cm^{-2} yr^{-1} (see Table 16.1), of which 25–30% is received in June. The isopleth for this mean of total solar radiation runs mainly across the middle of the tundra zone, bending a little southward in the west in the Atlantic area and deviating northward further east. At the northern border of the tundra, the amount of solar radiation is about 63 kcal cm^{-2} yr^{-1} in the center and up to 80 kcal cm^{-2} yr^{-1} in the east. The southern border of the tundra runs at various latitudes in different regions. In Europe it runs at about 67–68°N, while in Taymyr the southern border is found at 72°N and in Chukotka tundra or tundra-like landscapes can be met at 63°N. Thus, the same subzones receive unequal amounts of solar radiation.

Most of the solar radiation in the Arctic is reflected from the ground surface, but the albedo varies widely. During the summer, it is about 20%, while in snowy tundra it is 80% and with fresh snow it reaches 85–95%. The highest absorption of solar radiation takes place in July, when albedo is at a minimum, while the total solar radiation is still high.

The main indicator of the heat conditions is the radiation balance at the ground surface – that is, the difference between the total radiation reaching the ground surface and the part radiated back into space. In other words, this is the quantity which can be utilized for the different processes taking place in the ground cover. The yearly amount of the radiation balance at the Arctic seacoast and in the polar desert on the islands constitutes only 2–5 kcal cm^{-2} yr^{-1}. In the tundra zone, it is 12–15 kcal cm^{-2} yr^{-1}, increasing to 20–25 kcal cm^{-2} yr^{-1} near its southern border and in the forest tundra. If one takes the mean value of radiation balance to be 15 kcal cm^{-2} yr^{-1}, it constitutes about 21% of total radiation. It is about 16% in the polar desert. This

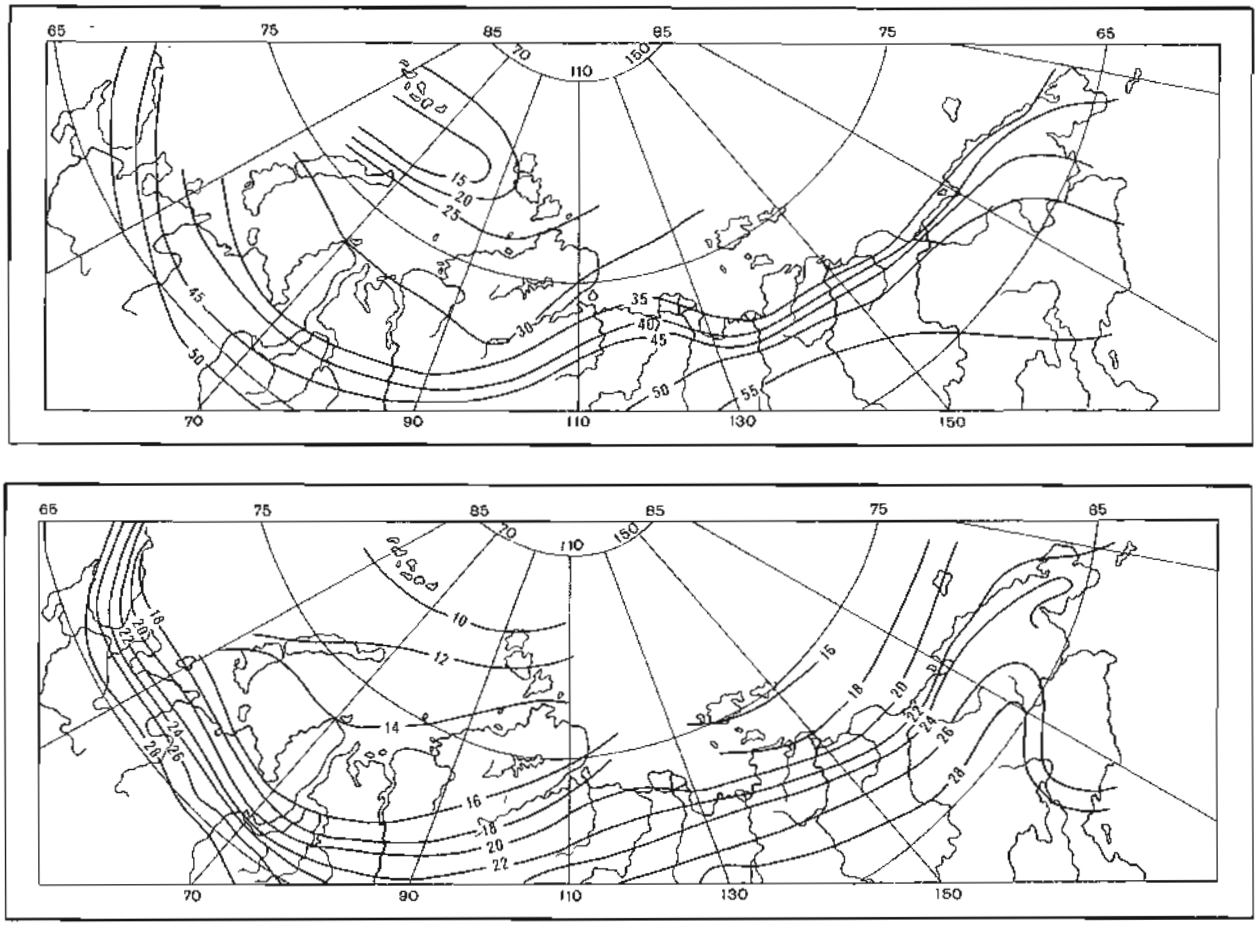


Fig. 16.4. Isolines of solar radiation (above) and radiation balance (below) in the Eurasian tundra for the period of thawing, kcal cm^{-2}. From Gavrilova (1981)

is primarily a result of the high albedo in the polar landscapes, which are under snow cover for the major part of the year.

The radiation balance also varies in different geographical regions of the Arctic (Fig. 16.4). This is particularly visible in the summer during the period of high biological activity. In central Siberia it varies from 14 to 16 kcal cm^{-2} for the thawing period, while in northern Europe, as well as in eastern Siberia and Chukotka, it is 18–24 kcal cm^{-2} (Gavrilova, 1981). The main features of arctic ecological conditions are due to the seasonal pattern of solar radiation (see Fig. 16.5). From November to February, the time of the arctic night, the mean monthly total radiation in the tundra is about zero (as can be derived from Table 16.1). For the month of March, it increases to 3–4 kcal cm^{-2}, but almost all is lost because of the backscattering effect and the albedo. During the lengthening of the arctic day in April, the total radiation increases to 8–9 kcal cm^{-2} and in May to 12 kcal cm^{-2}. However, at this time, snow cover reflects the major part of the radiation, so that the radiation balance at the ground surface remains very low (about 0 kcal cm^{-2} in April and 1–3 kcal cm^{-2} in May). In June, total radiation increases up to 14 kcal cm^{-2}. During this time, however, the albedo drops sharply as a result of the ground being almost bare and the diminishing reflective capacity of the melting snow. The June radiation balance is thus 5–6 kcal cm^{-2}.

Radiation balance reaches a maximum (8–10 kcal cm^{-2}) around the middle of July, in spite of the total radiation becoming somewhat less than in June. The radiation balance again falls during August and September.

The main characteristics of the solar radiation pattern in the Arctic are the following. First of all, the graph representing the radiation balance has a single peak. It rises steeply from May to July and

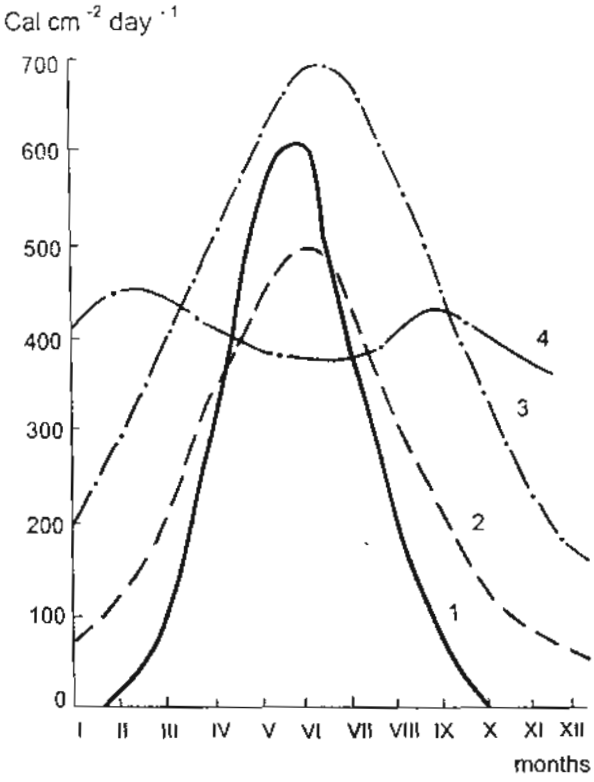


Fig. 16.5. Total seasonal radiation in different climatic belts. 1, arctic tundra, Resolute Bay, Parry Archipelago, 75°N; 2, taiga, Sverdlovsk, 57°N; 3, subtropics, Lisbon, 39°N; 4, equatorial belt, Singapore. From *Agroklimaticheskyi Atlas* (1972).

drops sharply during August and September. For that reason, the period of comfortably high temperatures in the tundra is very short. This contributes to an extraordinary dynamics of the seasonal development of the living organisms and to short phenological periods. Secondly, there is a clear difference in time between the peak of total radiation and that of radiation balance. In April and May, the quantity of solar radiation in the tundra zone is equal to the monthly mean in subtropical areas, while an immense quantity of energy is lost to biological processes because the radiation balance is still very low. When solar radiation can be effectively utilized by living organisms, it is already beginning to decline.

Heat and humidity

The annual heat supply depends on the radiation balance at the ground surface, although not all of it is equally important for living organisms. The main role is determined by the summer temperature which is the main factor for zonation. The winter temperatures are strongly dependent on the degree of continentality – that is, remoteness from a warm ocean not covered by ice. In consequence, the mean annual air temperature does not correctly reflect the conditions for life. Thus, in the polar desert in the far north of Novaya Zemlya, the mean annual air temperature is −7.6°C, approximately the same as in the typical tundra. The mean July temperatures of these regions, however, differ from each other by 4°. Northern Novaya Zemlya is located in the sphere of influence of warm oceanic currents, which explains the similarity between the regions in mean yearly temperatures. In the central Siberian arctic region, the differences between annual temperatures in the polar desert and in the southern tundra are only 1–2°C, whereas the mean July temperatures differ by 10°C (Fig. 16.6). On the whole, the mean yearly temperatures are highest in the outskirts of Eurasia (in northeast Europe and in the Chukotka (−6 – −8°C)) and much lower in its central part (−12 – −14°C). The same pattern can be observed in the January air temperature. The least cold part of the Arctic in winter is the coast of the Barents Sea (Barentsovo More) with −8 – −10°C for the coldest month. On the tundra coast of central and eastern Siberia, the mean January temperature is −30 – −35°C, while in

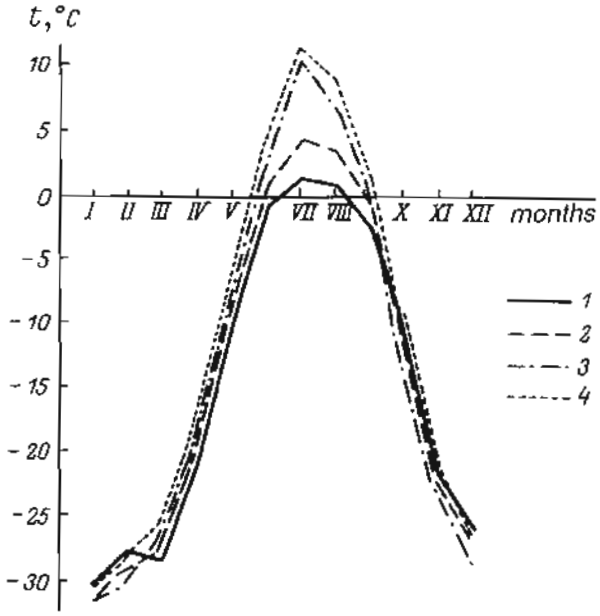


Fig. 16.6 Mean monthly temperatures in the different subzones of the tundra zone and in the polar desert in Taymyr. 1, polar desert; 2, arctic tundra; 3, typical tundra; 4, southern tundra. From Matveyeva and Chernov (1976)

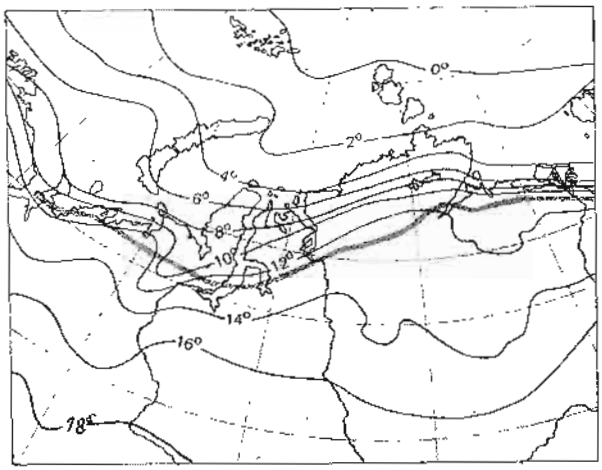


Fig. 16.7. Mean July isotherms (°C) over the Russian lowland and Siberia. Thick line is the boundary of the tundra zone. From Chernov (1985).

the extreme northeast of Asia (Chukotka) it is again higher and reaches −18 – −25°C (Agroklimaticheskyi Atlas Mira, 1972).

The northern border of the tundra zone coincides with the +1.5°C July isotherm and the southern border with +10°C. In the Taymyr, Gydan, and Yamal peninsulas where all the three tundra subzones are represented, arctic tundra is limited in the south by a mean July temperature of +5°C, typical tundra by +10°C. In eastern Siberia and Chukotka, the summer temperatures of the corresponding subzones are 2–5°C lower than in western and central Siberia. This is understandable because of the strong cooling influence of the sea, in spite of a higher radiation balance in comparison to the central parts of the arctic basin.

Maximum temperatures in the tundra can be very high, but not for a prolonged time. For example, in northern Taymyr the air temperature in July may reach 20°C and the absolute maximum at the latitude 73°N has been measured as high as 29°C. A still higher maximum temperature of 33°C has been registered on the eastern Siberian coast. The absolute temperature maximum in the polar desert at Cape Chelyuskin is 24°C. In southern tundra and forest tundra, the maximum air temperature can stay at 25°C for more than a week.

A significant detail of the temperature regime in the Arctic is the very wide variation in temperature. This can easily be seen from the mean monthly summer temperatures in the tundra zone when compared to those at more southerly latitudes (see Fig. 16.7). Thus, in the Bol'shezemel'skaya Tundra, the mean July temperatures vary from 6 to 12°C over a distance of 300 km. The July temperatures across the Russian lowland stretching 2000 km from the Arctic Circle down to the 50th parallel and including four natural zones vary by almost the same amount (13–20°C). In Taymyr at the limits of the tundra zone with a distance of 700 km, the difference in mean July temperature reaches 10°C (2–12°C), while in the territory of central Siberia, twice as large, it is only 6°C (12–18°C). A wide variation in the climate of arctic areas is reflected in the structure of the landscape and the organic life of the tundra and also determines the wide differences between subzones.

One of the most decisive factors for the development of organic life in the tundra is the length of the summer period. The date when the mean air temperature increases to above zero differs by 20 days in central regions of the tundra belt, from about June 10 in the southern tundra and the forest tundra to the beginning of July in polar desert. Similar differences are found at the end of the growing season, which ranges from the beginning of September in the north to about September 20 in the southern parts of the tundra. Thus, the frost-free period or growing period lasts 2 months or less in the polar desert and 3.5 months in the southern parts of the tundra. Approximately the same length of growing period is found in eastern Siberia and in the Chukotka tundra. In northeastern Europe, the frost-free period is strongly influenced by the unfrozen Atlantic Ocean. That is why the growing period in western arctic regions lasts for 4.5–5 months (from about May 20 to mid-October).

Although the main factor for the tundra zonation is solar radiation, it is also dependent on precipitation, which varies with latitude and longitude, with the geographical conditions, and with the distance from the sea. The highest precipitation in the area considered, 450–500 mm yr^{-1}, has been registered on the coast of Barents Sea, the lowest precipitation, 200 mm yr^{-1}, on the arctic coast in eastern Siberia. By latitude, precipitation is distributed as follows (data for the central Siberian region): 150–200 mm in the polar desert, 200–250 mm in the arctic tundra, and 300–350 mm in the typical and southern tundras and in the forest tundra. Orographic influence on the distribution of

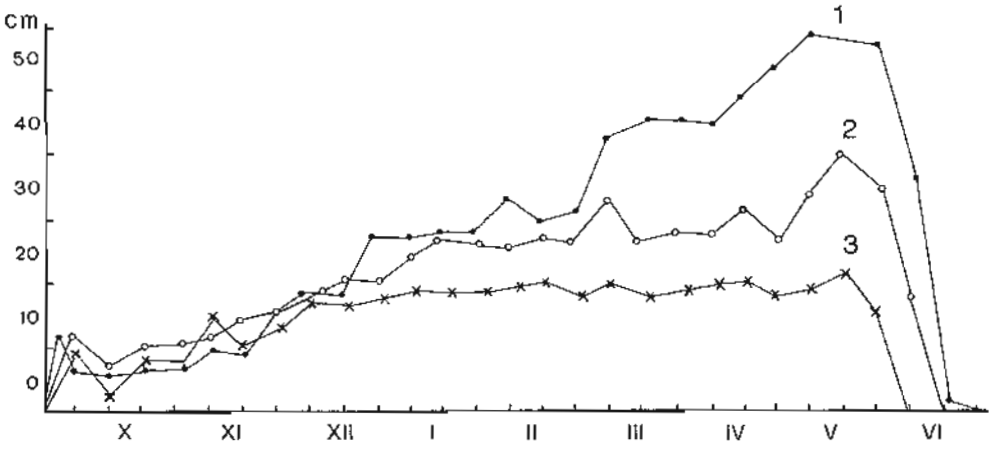


Fig. 16.8. Snow depth on different elements of the nanorelief in frost-boil tundra communities at Taymyr (Tareya, 1968). 1, troughs; 2, rims; 3, patches of bare ground.

precipitation is clearly seen for instance in the Byrranga mountains in the central part of Taymyr, where the annual precipitation is 450–500 mm, while only 300–350 mm has been recorded in the surrounding plains. Approximately one-third of the annual precipitation falls in the form of rain in July–August.

In the tundra zone, snow lasts 200–280 days. It appears in various regions from the middle of September to the middle of October. Stabilization of the snow cover takes 10–15 days. The duration of snow cover has a maximum in the central and eastern parts of the tundra belt and reaches a minimum closer to the Atlantic. On Taymyr, the snow stays from 260 days in the south to 280 days in the north, while in the Bol'shezemel'skaya Tundra and southern Novaya Zemlya it lasts about 240 days and in the northern part of the Kola peninsula about 200 days. On the whole, the slight precipitation causes the snow cover to be relatively thin; it quickly increases during the autumn, then slowly reaches a maximum at the end of April. The thickness of the snow cover within the tundra zone varies between 10 and 50 cm, but in the majority of places it is 20–30 cm thick. Similar values have been observed in the forest tundra. It is less in the north of the tundra zone and in the polar desert (20–25 cm) than in the flat parts of the tundra further south (40 cm). In northeastern Europe and in Chukotka, snow cover is about 50–60 cm. Because of the constant and strong winds, the thickness of snow cover is not the same in different parts of a relief; even the nanorelief affects it (Fig. 16.8). It can vary from 0 cm on ridge tops and banks to several meters in deep and narrow valleys. Snowmelt starts at the beginning of May in western parts of the tundra zone and at the beginning or the middle of June on the coast of the Laptev Sea (More Laptevykh), but not before the end of June or the beginning of July on the arctic islands. There are snowbeds on hill slopes, among rocks, and in narrow valleys that do not melt completely during summer, and snow patches are preserved until the appearance of new snow cover. Snow may fall even in the middle of the growing period in July and August, but it usually lasts no more than 1–2 days. These summer snowfalls are not very dangerous for living organisms.

High relative air humidity, about 80–90%, is very typical in the Arctic. It is somewhat higher in the north (84% in winter and up to 95% in summer in the Severnaya Zemlya archipelago, with the mean value being 90%) and lower in the south (from 71% in summer to 86% in winter in the southern tundra and forest tundra on Taymyr, with an average of 78%).

The abundance of moisture in the tundra is the result of the low rate of evaporation. The correlation between the amount of heat and atmospheric humidity is reflected in the hydrothermal indices. The widely known "radiation aridity index" of Budyko (1956) is the ratio between radiation balance and total yearly precipitation in terms of latent heat of evaporation. This index indicates the possibility of water accumulation under certain radiation conditions. Territories with an index equal to 1 are most favorable for organic life. An index of about 1 is typical for landscapes of the

TABLE 16.2

Humidity conditions at various latitudes

"Zonal" type of landscape	Amount of precipitation (mm yr^{-1})	Radiation index of dryness
Polar desert	110	0.1
Arctic tundra	200	0.2
Typical tundra	250	0.3
Taiga	370	0.6
Mixed forest	450	0 8
Forest steppe	380	1.0
Desert	100	3.0
Tropical forest	1000	0.9

From Kalesnik (1970) and Ryabchikov (1972)

temperate zone, such as deciduous forest and forest steppe (Table 16.2). In the tundra, this index ranges from 0.4 to 0.2, while in the polar desert 0.2 or less is measured, which clearly indicates that the temperature in these zones is not high enough to evaporate the annual precipitation.

The lack of heat is the decisive factor causing the extremeness of living conditions in the Arctic, whereas in hot deserts there is enough heat, but little moisture. In order to survive in a hot desert, it is necessary for an organism to be able to extract water, store it, and conserve it for prolonged periods of time. The lack of heat in the tundra is practically impossible to overcome by any kind of adaptation. Even partial adaptations to cold are limited and are not as diverse as adaptations to drought. Heat is the main condition for accomplishing all biological processes; lack of it inhibits life in any form. Therefore, the organic life in the tundra zone is limited in the number of species and types of adaptations, but it is spread over the landscape more uniformly than life in a hot desert.

In spite of the general peculiarity of the climate in the tundra zone, it is doubtful if there are any unique factors in the environment which affect all groups of organisms. Although lack of heat and low temperature are characteristic traits of living conditions in polar landscapes, the minimum temperatures in tundra are not extreme enough to exclude a large number of plants and animals, because almost no organisms are subjected to the direct effect of frost during winter. At that time they are not active, they live mainly under the snow or migrate to the south. The freezing temperatures in the tundra zone are, in reality, not as severe as in many other, more southerly, continental areas (see Table 16.3), where many birds and mammals hibernate, including those which have

TABLE 16.3

Climatic data for different regions of Siberia

Site	Temperature (°C)			Total day-degrees ($t° > 0°C$)	Amount of precipitation (mm y^{-1})
	Mean annual	January mean	July mean		
Polar deserts					
Domashnyi Island	−14.7	−28.4	0.7	27	110
Russkiy Island	−14.3	−29.2	1.2	62	140
Cape Chelyuskin	−14 5	−29.6	1.5	80	139
Arctic tundras					
Belyi Island	−10.4	−23.4	4.1	372	171
Dikson Island	−11.5	−26.3	4.6	392	192
Maria Pronchishcheva Bay	−14.0	−31.2	4.0	283	163
Typical tundras					
Cape Kamennyi	− 9.4	−24.4	8.1	758	250
Gydoyama	−11.2	−27.6	9 6	707	212
Ust'-Tareya	−13.4	−31.3	10.5	657	204
Forest tundra					
Khatanga	−13.4	−33.8	12.3	852	187
Northern taiga					
Verkhoyansk	−15.7	−48 6	15.2	–	–
Middle taiga					
Yakutsk	−10.3	−43.2	18.7	–	–

Data given in the USSR Climate Directories.

migrated from the tundra. The inhabitants of the taiga are, actually, more cold-resistant than the animals of the tundra. The plants in the tundra are covered by snow during winter, while the uncovered trees and bushes of the taiga are able to endure extremely low temperatures. As for arctic invertebrates, there is no essential difference in apparent cold-hardiness between them and those typical of more southerly landscapes (Lozina-Lozinskyi, 1972).

One of the most characteristic traits of the polar environment is the almost continuous daylight during summer. However, for the life of the majority of organisms this is actually of greater importance in the forest tundra and in the northern taiga than in the tundra zone, especially in areas with a continental climate as, for instance, along the lower reaches of the Khatanga, the Anabar, and the Lena rivers where forested landscapes extend all the way up to 71–72°N. There the climax of plant growth and the annual life cycles of animals (especially processes related to reproduction) occur during the brightest time of the year, in June and at the beginning of July. In the major part of the tundra zone, "summer" does not start until the beginning or middle of July, when the nights begin to darken again.

The most negative factor for living conditions in polar lands is the shortness of the period above 0°C that permits growth of plants and active life of poikilothermal animals, as well as for reproduction, growth, and development of the majority of homoiothermal animals. However, this factor is unimportant for some groups. The brevity of the arctic summer presents great difficulties for the reproduction of many, but not all, birds. Tundra plants on the other hand, are able not only to complete their seasonal cycle, but even to display some seasonal aspects. Thus, in spite of the general severity, the conditions in the tundra landscape provide acceptable habitats for species with different life styles and converging phenology where the organisms are able to survive in specific habitats, in which the general climatic conditions undergo a greater or lesser transformation.

In spite of the general poverty of organic life in the tundra, it harbors species displaying diverse kinds of morphology, physiology, and behavior. However, it is doubtful whether there are any unique and specifically adapted forms which are sharply distinguished from animals and plants inhabiting other zones.

Fig. 16.9. Thermoabrasion cliff on Big Begichev island (Ostrov Bol'shoy Begichev) in the Laptev Sea. Permafrost and ice under a thin layer of active soil.

Permafrost and nanorelief

The structure of communities and the functioning of ecosystems are under the influence of climatic conditions both directly determining the intensity of certain processes, such as photosynthesis, growth, trophic activity, etc., and indirectly causing effects mainly through specific structures of landscapes. Among these, permafrost is of great importance.

There is continuous permanently frozen ground in almost all areas of the tundra zone in Eurasia (Fig. 16.9), but presence of permafrost is not specific for the tundra landscapes. In Siberia, the border of permafrost stretches southward to the steppes. On the other hand, it is not continuous in northern Europe. Permafrost is generally absent in the Kola peninsula, but may be found in patches of mires in northeastern Norway.

Several facts associated with permafrost are of great significance for all living organisms of the tundra – for instance, the date of beginning and the duration of the thawing of upper soil layers, the depth of seasonal thawing, and the dynamics of this process. The thawing begins just after snowmelt when the daily air temperature passes zero. These dates can vary over a range of 20 days between southern and northern regions. In different years, the date at any given site can also vary within the same range, depending on the weather. Thawing usually starts in the second or third week of June. The most intensive period of this process lasts about one month, independent of the date when it started. The permafrost level reaches its

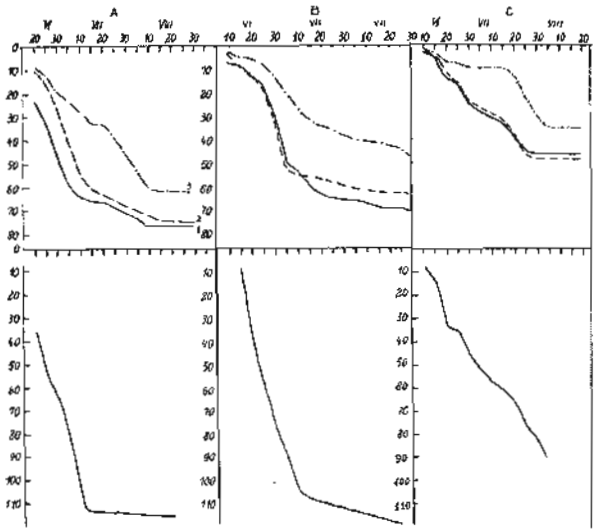


Fig. 16.10. The dynamics of permafrost thawing in different tundra subzones on Taymyr. A, southern tundra (Kresty, 1976); B, typical tundra (Tareya, 1969); C, arctic tundra (Dikson, 1979). Upper row of figures shows "zonal" communities on "plakor" (1, patches of bare ground; 2, rims; 3, troughs). Lower row shows meadows on southern slopes.

maximum depth usually by the beginning of August (Fig. 16.10). This depth depends on the latitude as well as on the position in the landscape. On a flat surface in the southern part of the tundra, the maximum depth of permafrost thawing is 80–90 cm. It is 70–80 cm in the middle part, 50–60 cm in the northern part of the tundra zone, and about 40 cm in the polar desert.

The greatest depth of thawing in the southern and typical tundra subzones, 120–130 cm, has been measured on southern slopes that are well heated. In the arctic tundra, however, there are no differences in thaw depth between a flat surface and southern slopes (Matveyeva and Chernov, 1977). The least depth of thawing is in peat bogs. Here, it amounts to 40–50 cm in the southern part of the tundra, whereas only 20 cm of the peat is thawed near the northern tundra border. Differences in the thaw depth of peat bogs in different years amount to only 10–15 cm, depending on summer weather. Only half of the soil profile is thawed during the period of the more intensive plant and soil invertebrate activity. The upper soil layers begin to freeze in autumn when the daily air temperature again goes below 0°C. The freezing begins from the soil surface, but a slight (3–5 cm) rise of the permafrost level has also been registered.

The appearance of the tundra landscape is more or less associated with permafrost. Generally, it has an adverse effect on the vegetation, causing soaking of the ground, mechanical impediment to the development of the root system, and damage of the vegetation cover under cryogenic processes. However, the vegetation also exerts an effect on the depth of the active layer, which means that there are always complicated and contradictory interrelationships between permafrost and vegetation. Under a denser plant cover, the heat-insulating properties increase and the soil temperatures decrease. The latter leads to a rise in permafrost, which worsens conditions for vascular plants in particular.

Because of permafrost, tundra areas have very peculiar forms of relief which are specific and different from those in other zones. Specific forms of such arctic micro- and nanorelief with regular repetition of elements are also responsible for the very peculiar pattern of vegetation on various scales found in tundra.

The most typical tundra landscape in the Siberian Arctic is a gently rolling plain, dissected by numerous watercourses and hollows, forming a network with many small pools and lakes occurring in groups. The pools appear as a result of local thawing of the permafrost (Fig. 16.11). Temporary watercourses, which flow only in spring during snowmelt, often erode ditches or gullies, forming short but not very deep ravines with crumbling walls. Their depths depend on the thickness of loose marine deposits.

A really flat surface extending more than a few square meters is very rare in the tundra zone, with the exception of wet boggy habitats and flood plains. In all other places, a nanorelief is always present. Miscellaneous cryogenic processes, such

Fig. 16.11. Tundra pool with dense cotton grass (*Eriophorum scheuchzeri*) on Taymyr.

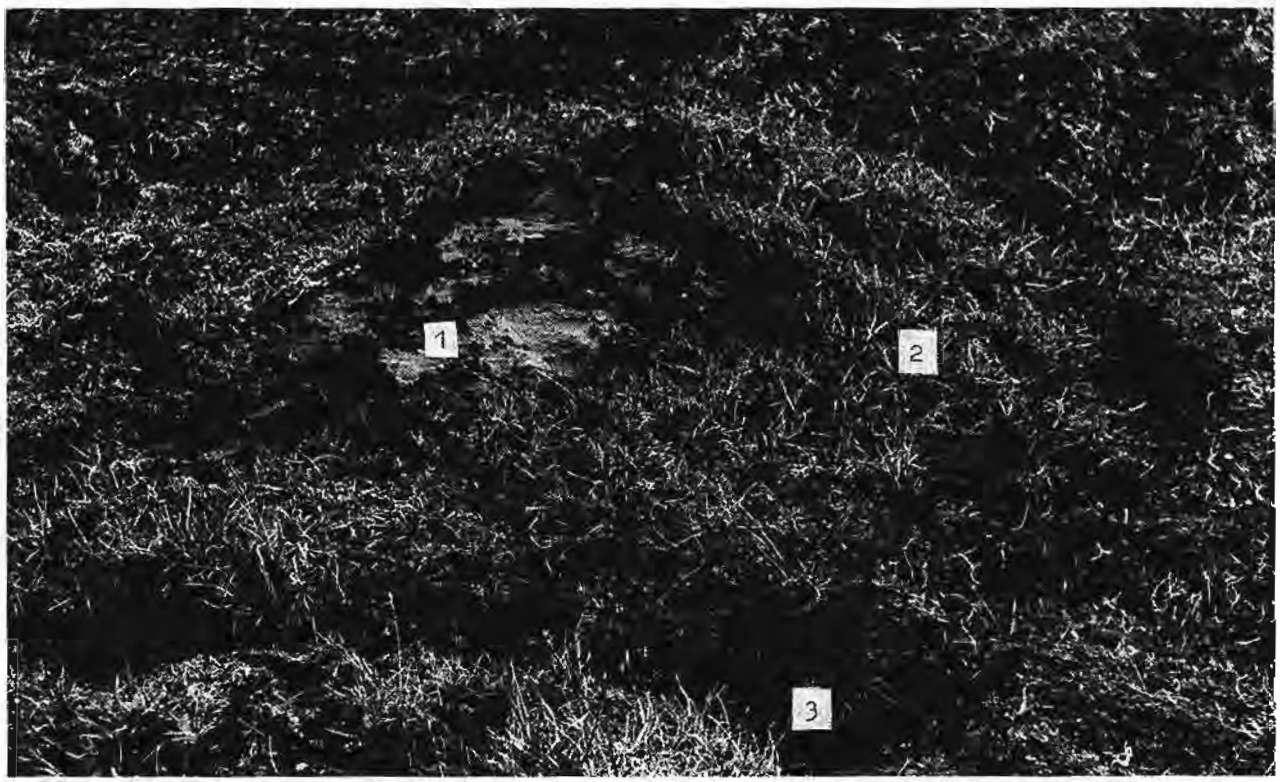


Fig. 16.12. Frost-boil *Dryas*–sedge–moss community 1, patch of bare ground; 2, rim; 3, trough.

as heaving, crack formation, soil sorting, solifluction, and expulsion, all lead to the formation of patterned ground (Washburn, 1956). This collective term mainly covers the symmetrical forms of arctic nanorelief, such as circles and polygons, medallions, networks and strips, which are responsible for the general heterogeneity of the living cover in tundra.

Typical in tundra are polygonal mires (Boch and Masing, 1983), with low-centered polygons 7–15 m across, rims 0.7–1 m in height and up to 2 m in width, and deep water-filled troughs along frozen cracks in the ground. A single polygonal mire may have 50–100 polygons. Other tundra mires have groups of flat-topped peat hummocks 1–10 m in diameter and 0.5–1.5 m in height.

Hummocky communities with a continuous but mosaic cover, caused by small hummocks 10–15 cm in height and diameters of 15–30 cm (occupying about 70% of the stand area) and troughs of 15–20 cm in width, are most common in the southern tundra subzone of Russia. No less typical for the central and southern parts of the tundra zone are frost-boil tundras, in Russian literature called spotted tundras (*pyatnistye tundry*) (Fig. 16.12). The main elements of their nanorelief are patches of bare soil (usually 50–70 cm in diameter), rims 5–10 cm in height that surround these patches, and troughs 15–30 cm in width and 10–15 cm in depth separating the rims of adjacent patches. The whole pattern of regularly repeated elements in frost-boil communities is similar in different parts of the tundra zone, but the size of the elements and ratio of their areas are not constant. From south to north, the size of soil patches, their number per unit area, and the proportion of bare ground become larger (Fig. 16.13). The best three-element structure is represented in the typical tundra subzone, where almost round patches of bare ground uniform in size are surrounded by well-pronounced closed rims and troughs that are rather wide and clearly concave. In the southern tundra subzone, patches are not round, rims are not high, and "troughs" are almost flat. In northern parts of the tundra (the arctic-tundra subzone), all the elements fuse together. The rims are usually not closed, which means that some patches may touch each other. Troughs are narrow and deep with vertical walls. This type is usually called polygonal tundra.

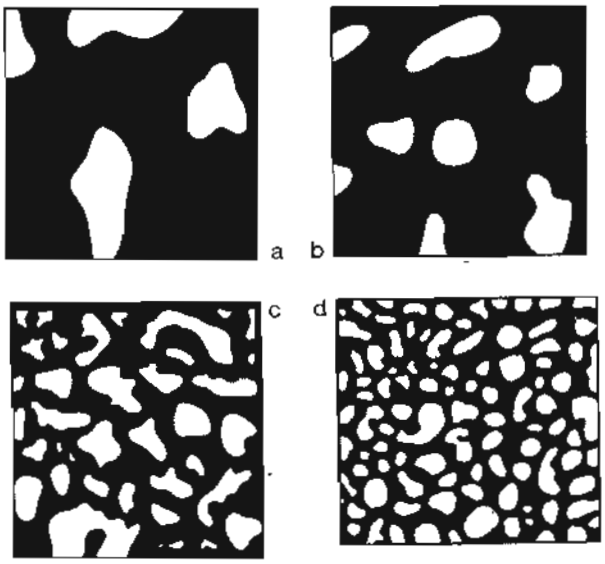


Fig. 16.13. Diagram of the distribution of patches of bare ground. a, southern tundra; b, typical tundra; c, arctic tundra, d, polar desert on Taymyr. Sample plot 5 × 5 m. From Chernov and Matveyeva (1979).

A very specific type of tundra microrelief is indicated by the Yakutian term "baidzharakhs" (Fig. 16.14). They are relic mounds 3–10 m in width and 0.5–6 m in height enclosing ice blocks, often arranged in rows. Their geographical distribution is closely related to the development of polygonal ice inclusions due to subterranean glaciation, and they are common for instance on the Novosibirskiye Islands. In Yakutiya, single large hydrolaccolithic mounds of 150–200 m in diameter and 70 m in height are more typical, locally called "bulgunnyakhs" (= "pingos" in the Canadian Arctic). They are covered by peat about 1 m thick above frozen mineral sediments, up to several meters thick, hiding a cupola-shaped mass of ice.

ZONATION AND DIVERSITY OF COMMUNITIES

Abiotic factors vary markedly not only between different tundra subzones, but also within each of the subzones, depending on the degree of oceanicity, continentality, and latitude, as well as on various elements of the landscape. It is known, for example, that steep southern slopes in Taymyr receive on average 1.5 times more direct solar radiation than a flat surface (Romanova, 1978). Differences of this order in the annual radiation balance correspond to displacement by a whole geographic zone.

Differentiation of the environment is reflected in the composition and structure of communities which are formed in different elements of the landscape. "Zonal" vegetation is the natural vegetation cover which most fully reflects the climatic conditions of the natural zone in question. The proper "zonal face" of the locality, therefore, is reflected by groupings of vegetation, soils, and animal communities on horizontal or slightly sloping well-drained areas, on which the hydrothermal regime corresponds to the climatic conditions of the zone in question. The term "plakor" was suggested by Vysotskyi (1909) for such areas. In the tundra zone, isolation of "plakor" elements is made difficult due to the peculiarity of the moistening regime in the presence of permafrost. We have taken the view of Aleksandrova (1971), who assigned the concept of "plakor" in the tundra zone to slightly sloping surfaces with average snow accumulation.

There are various elements of plant cover defined as "intrazonal" in Russian terminology between the typical "zonal" communities developed on "plakor". Categories of intrazonality are relative and conventional, and in nature there are of

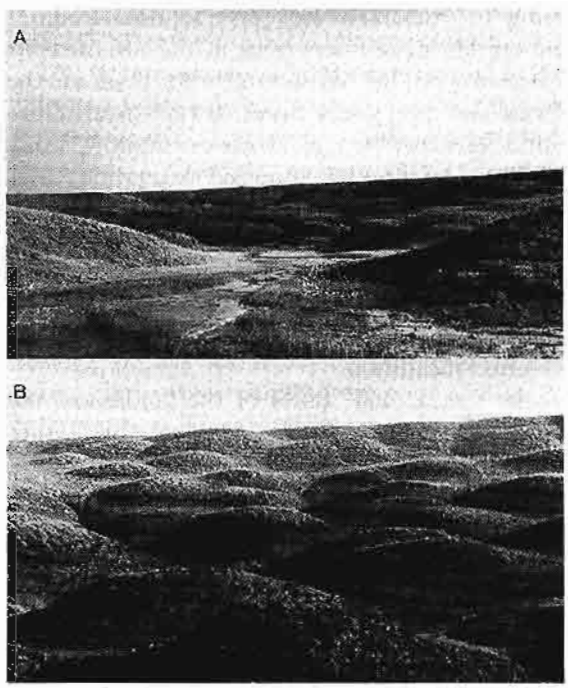


Fig. 16.14. Baidzharakh hummocks by Rogozinka River, Taymyr. A, general view; B, close view.

course transitions between "zonal" and "intrazonal" communities. The most rigorously substantiated scheme of coordination of "zonal" and "intrazonal" plant communities is that of Alekhin (1951). By slight modifications of the scheme by Alekhin, it is possible to distinguish the following categories of communities in connection with their position in the landscape (Chernov, 1975).

(1) "Zonal": the communities occupying horizontal and slightly inclined surfaces with average snow accumulation and without traces of stagnant water (on "plakor"). These are the tundra communities proper – for instance, willow and birch stands in the southern tundra subzone, sedge–mossy small hummocky communities and frost boils and cotton-grass tussock communities in the typical tundra subzone, and herb–mossy polygonal communities in the arctic tundra subzone.

(2) "Extrazonal": areas of "zonal" types of communities located beyond the limits of their general distribution on "plakor" – for instance, the forest islets on riverbank terraces in the subzone of southern tundras, thickets of tall shrubs (willow and alder groves) along the slopes and valleys, dwarf birch in shallow depressions in the typical tundra subzone, and communities analogous to polar deserts in the arctic tundra subzone.

(3) "Intrastenozonal" ("intrazonal" proper according to Alekhin): very diverse non-"plakor" communities mostly occurring in the tundra zone or extending not far beyond its limits. Such are the hillocky and polygonal mires, dwarf-shrub communities of *Cassiope* and *Dryas* on shallow, stony soil (fell-fields), and the snowbed vegetation.

(4) "Intrapolyzonal" ("azonal" according to Alekhin): communities not adapted to any particular zone, but distributed within the limits of many zones. Such are the seashore thickets of *Elymus arenarius, Rhodiola rosea*, and some variants of herb–grass meadows.

In the "intrazonal" parts of the landscape, the gradient of climatic factors is "smoothed out" (Chernov, 1975). This plays an enormous role in the distribution of plants and animals. On the one hand, the non-"plakor" elements serve as refuges where fluctuations of climatic factors are smoothed out in time and space. On the other hand, a greater diversity of conditions within the variegated range of "intrazonal" groupings appears to stimulate the intensity of species formation. In the process of development of flora and fauna, they play the role of suppliers to the "plakor" communities (Yurtsev, 1966; Chernov, 1975, 1978b).

In arctic regions, with their heat deficiency, differences in the hydrothermal regimes in the "zonal" and "intrazonal" communities are critical. This aspect, therefore, will be constantly taken into account in characterization of the parameters in subsequent pages.

Tundra zone

Southern tundra subzone

The southern tundra lies between two sharply differing biomes: the forested regions with trees predominating on the one side and treeless areas on the other. The forest tundra separates these two biomes and is the ecotone between the two contrasting types of landscape. The southern tundra is a genuine subzone of the tundra zone, which has long been reflected in various schemes of latitudinal division of northern territories (Berg, 1928; V.N. Andreyev, 1932, 1935; Sambuk and Dedov, 1934; Gorodkov, 1935; Sambuk, 1937; Chernov, 1975; Chernov and Matveyeva, 1979, 1986).

The southern tundra subzone is represented over almost the entire territory of northern Eurasia, except for those regions where the mountains are in close proximity to the seashores (see Fig. 16.1). It is the widest subzone in the European part of the area (apart from the Kola peninsula) and on Chukotka, but is considerably narrower in eastern Siberia. Its southern boundary is usually drawn along the northern limit of distribution of large tracts of forest; it mainly coincides with the 10–12°C July isotherms. The northern boundary is drawn according to the distribution of comparatively dense shrub thickets on the well-drained, nearly flat "plakor"; it approximates the 8–10°C July isotherms.

In this subzone, along the riverbanks, it is still possible to come across some areas of sparse tree growth, krummholz, or prostrate woodlands. Yet, on the "plakor" only solitary specimens of those species grow which form the forest border in each particular region of Eurasia: *Betula tortuosa, Chosenia arbutifolia, Larix cajanderi, L. gmelinii, L. sibirica, Picea obovata, Populus balsamifera* and *P. suaveolens*.

The most important feature of the plant cover of the southern tundra subzone is the presence of shrub communities on "plakor" (Fig. 16.15). In different sectors of the Arctic, they consist of

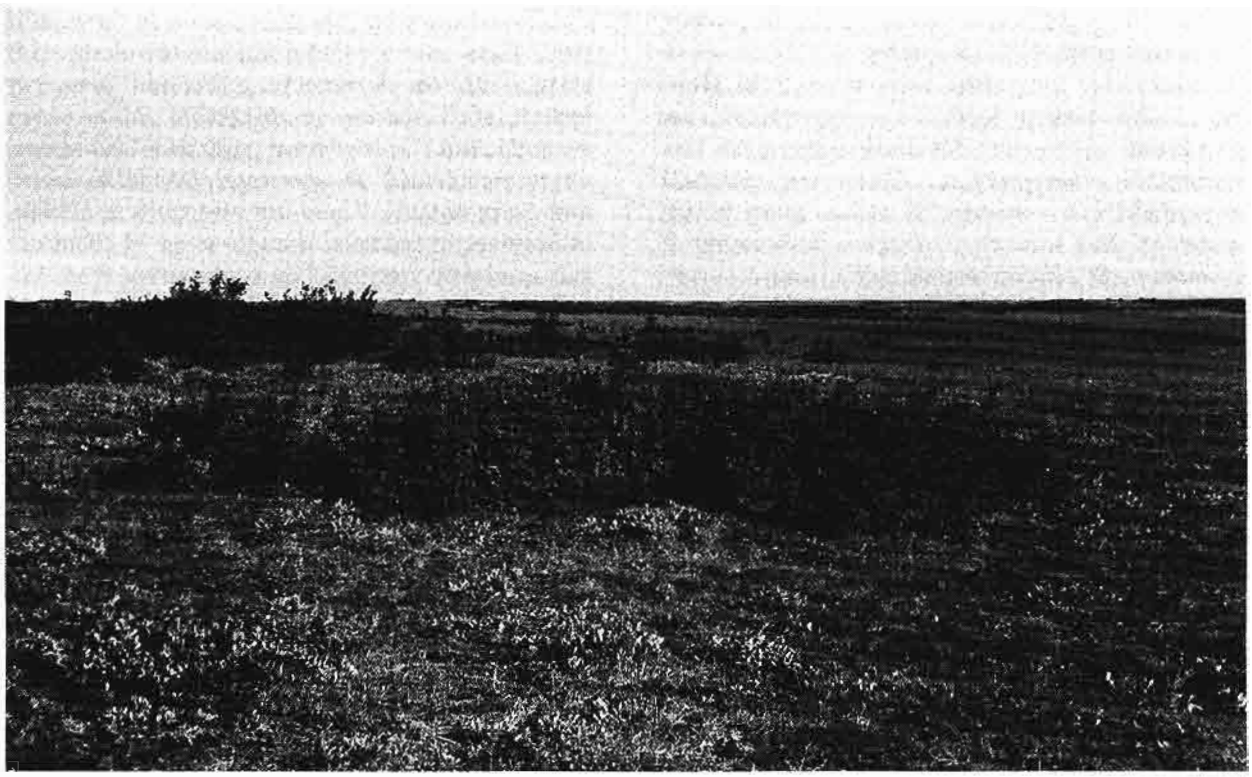


Fig. 16.15. Landscape of southern tundra at Kresty, Taymyr.

several species of birches (*Betula exilis*, *B. glandulosa*, *B. middendorfii*, *B. nana*), willows (*Salix alaxensis*, *S. glauca*, *S. lanata*, *S. lapponum*, *S. phylicifolia*, *S. pulchra* and others), and alder (*Alnaster fruticosus* and *Alnus crispa*). On the "plakor", the majority of shrubs are 0.5–0.8 m high, which is determined by the depth of the snow cover, although the alder shrubs can reach 1.5–2 m. The same height is reached by shrub willows in river valleys.

In the field layer of the "zonal" communities, predominant species are the dwarf-shrubs *Cassiope tetragona*, *Dryas octopetala*, *D. punctata*, *Empetrum hermaphroditum*, *E. subholarcticum*, *Ledum decumbens*, *Vaccinium uliginosum* ssp. *microphyllum* and *Vaccinium vitis-idaea* ssp. *minus*, as well as the sedges and cotton grasses *Carex ensifolia* ssp. *arctisibirica*, *C. globularis*, *C. lugens*, *Eriophorum angustifolium* and *E. vaginatum*.

The ground cover includes the mosses *Aulacomnium turgidum*, *Dicranum congestum*, *D. spadiceum*, *Hylocomium alaskanum*, *Pleurozium schreberi*, *Polytrichum commune*, *P. juniperinum*, *P. strictum*, *Racomitrium lanuginosum*, and *Tomenthypnum nitens*, and some liverworts like *Ptilidium ciliare* and *Tritomaria quinquedentata*.

The lichens are abundantly represented by fruticose and foliose forms, such as *Cetraria cucullata*, *C. islandica*, *C. laevigata*, *Cladina arbuscula*, *C. rangiferina*, *Cladonia amaurocraea*, *C. gracilis*, *Dactylina arctica*, *Peltigera aphthosa*, *P. rufescens*, *Stereocaulon alpinum*, *S. paschale* and *Thamnolia vermicularis*.

The chief manifestation of the severe polar climate in the southern tundra subzone is the absence of real arboreal vegetation. In other respects, the southern tundras are comparatively rich communities. The situation of the southern tundras near important biogeographic boundaries leads to a great heterogeneity of their biota because of involvement of species from different "zonal" areas.

In the southern tundra, there is a substantial proportion of nonarctic elements in both flora and fauna. They reach high numbers in the "zonal" and, especially, in the "intrazonal" communities. The proportion of boreal and polyzonal plant species is highest among the cryptogams. They

include all the soil algae, most species of mosses, and many cosmopolitan species of lichens which are typical for the tundra zone as a whole. However, in the southern tundra, true forest mosses are also found: *Climacium dendroides*, *Dicranum scoparium*, *Hypnum pratense*, *Pleurozium schreberi*, *Rhytidiadelphus triquetrus*, as well as many boreal species of bog mosses: *Sphagnum fimbriatum*, *S. nemoreum*, *S. squarrosum*, *S. teres*, and *S. warnstorfii*. Boreal and polyzonal species amount to one-third of the local flowering-plant floras. The majority of these species are solitary representatives of families and genera. Therefore their presence increases the floristic richness not only at a species level, but also at higher taxon levels.

In the animal kingdom, the proportion of non-tundra forms is so high that they obscure the tundra elements proper. This is well seen among taxonomic and ecological groups, especially in birds and in some families of insects. The majority of boreal and polyzonal species are chiefly or exclusively associated with "intrazonal" communities and biotopes: mires, meadows on southern slopes, and river valleys. However, some of them are connected with "plakor" shrub communities. The most typical inhabitants of the southern tundra subzone are hypoarctic species (Yurtsev, 1966; Chernov, 1978b; Eskov, 1986; Tolmachev, 1986).

The role of hypoarctic species in the southern tundra plant cover is greater than in all other tundra subzones or in any other latitudinal subdivisions. Most of the abovementioned shrubs and dwarf-shrubs belong to them, as well as a number of mosses. The majority of these plants find their optimal ecological conditions only here, and in this territory attain maximum density. The proportion of hypoarctic species is nearly as great among the animals and include a number of birds (*Anthus cervinus*, *Emberiza pusilla*, *Gallinago stenura*, *Lagopus lagopus*, *Limosa lapponica*, *Tringa erythropus*) and also several invertebrates (e.g., the spider *Alopecosa hirtipes*, the bumblebee *Bombus cingulatus*, and the carabid *Carabus truncaticollis*) as well as some mammals (e.g. the vole *Microtus middendorfii*). These species are most typical of the animal communities of the southern tundra subzone, and here their numbers are higher than elsewhere in their distributional areas. The northern boundary of distribution of the majority of these species coincides with the areas of shrub thickets on well-drained areas of "plakor".

In the southern tundra subzone, the hemiarctic species (whose growth optimum falls in the middle part of the tundra zone) dominate the plant cover along with the hypoarctic ones and primarily include such species as *Arctophila fulva*, *Carex ensifolia* ssp. *arctisibirica*, *Cassiope tetragona*, *Dryas octopetala*, *D. punctata*, *Dupontia fisheri*, and *Salix reptans*. There are also quite a number of hemiarctic animals, though some of them are still markedly restricted by competition from boreal and polyzonal species.

In the southern tundra subzone, the arctic species typical of the northern part of the tundra zone are either absent or restricted to more unfavorable biotopes, such as the snowbeds.

As a whole, the southern tundra may in many ways be grouped with forest tundra both floristically and faunistically, and in Asia even with northern open woodland. Among the commonest species, however, are those which dominate in the middle part of the tundra zone. This unites the southern tundras with the other tundra subzones to constitute a single zone.

The communities of the southern tundra are characterized by many important peculiarities in both vertical and horizontal structure. Over major parts of its range, this subzone may be called the tundra shrub subzone, as has been done by many investigators. Here, one may find the most complete stratification in the tundra zone: a shrub layer (0.5–2.0 m high), a dwarf-shrub and grass layer (5–20 cm), and a lichen–moss layer (5–10 cm thick). These are at the same time the tallest communities, transitional between the arboreal communities with many layers and the treeless ones with few. There is much leaf litter in the southern tundra. Therefore, a typical feature of the vertical structure of the animal population is a well-developed complex of litter invertebrates. Especially representative are gnat larvae of the family Bibionidae which live in large colonies and feed on leaf litter. Even ants (represented by *Leptothorax acervorum*) are still common as far north as this subzone. The complex of inhabitants of the grass layer is better developed in the southern tundra than further north. Among them are forms adapted to inhabit only the grass stratum, such as the cicadas (*Bathysmatophorus*, *Psammotettix*, *Streptanus*), the bugs (*Chlamydatus*, *Orthotylus*, *Platypsallus*), the springtails (*Sminthurus*), and others.

The horizontal structure is very diverse. On the "plakor", there are shrub thickets of different

species of alder, birches, and willows alternating with areas without a shrub layer. The plant cover in "zonal" communities may be continuous because of the development of dense moss cover which has a mosaic pattern due to the growth forms of the dominant mosses. Yet, there are also communities where the cover has been destroyed, particularly in the spotted tundras. In "zonal" communities of the southern tundra, patches of bare ground are larger than anywhere else in the tundra zone (0.8–3.0 m^2), and their density is about 15 per 100 m^2. Plant cover is being actively restored within the patches and the bare ground occupies not more than 20–30%.

The "intrazonal" communities differ very sharply from the "zonal" communities on "plakor". "Intrazonal" communities typical of the southern tundras include large and flat palsa bogs, homogeneous mires, and swampy runoff hollows in which the dense homogeneous grassy cover is made up of cotton grasses and sedges and the moss cover consists mainly of hygrophilous species such as *Calliergon*, *Drepanocladus*, and *Meesia*. The peat hillocks are formed by *Sphagnum* spp. The northernmost outpost of boreal meadows with *Allium schoenoprasum*, *Chamaenerion angustifolium*, and *Galium boreale* can be found in the river valleys. On southern slopes, a rich meadow vegetation is made up of grasses, legumes and other herbs, including both arctic and boreal species.

Some forest islets can also be found, as "extrazonal" inclusions, in the European part of Russia; for example, the forest island More-Yu at 67°50′ with *Betula tortuosa* and *Picea obovata*, and on Taymyr the forest Ary-Mas at 72°30′ with *Larix gmelinii*. Such forest tracts existed until the 1950s on the island Tit-Ary in the lower reaches of the river Lena; while groves of *Populus suaveolens* are not infrequent on Chukotka.

In the northeastern part of the southern tundras of Russia, large territories are occupied by tussock communities of *Carex lugens* and *Eriophorum vaginatum*.

In spite of the predominance of circumpolar species, the southern tundras in different sectors of the Arctic differ much more in species composition than the two northern subzones and are more arctic in Siberia than in Europe. The nontundra elements present strongly depend on the latitude as well as on the forest type situated to the south of the tundra.

Typical tundra subzone

This subzone (in Russian literature also called the moss–lichen tundra subzone) in Eurasia is well pronounced on the Taymyr, Yamal, Gydanskiy, and Yugorskiy peninsulas, between the rivers Khatanga and Olenëk, and between the Yana and the Kolyma rivers. Elsewhere, it is represented fragmentarily in narrow belts along the sea coast. It is absent on the mainland west of the Yugorskiy peninsula. The boundaries of the subzone approximately correspond to the 8–10°C July isotherm in the south and 5–6°C in the north.

This subzone is the incarnation of that type of landscape which is called tundra (Fig. 16.16). Here, one cannot find even a solitary tree, and on "plakor" there are no tall and closed shrub thickets. The latter are typical only of "intrazonal" biotopes, such as river valleys, rivulets, and lake depressions. On the "plakor", low shrubs such as *Salix glauca* and *S. reptans* grow up to 20 cm high, many with a semiprostrate form (*Betula nana*, *S. pulchra*).

The typical tundra is a kingdom of mosses which manifest themselves as true transformers of the environment. The moss turf covers the soil in a layer 5–10 cm thick. It is made up of many species forming a mosaic. About 10 species are comparatively richly represented, among which the most important are *Aulacomnium turgidum*, *Hylocomium alaskanum*, and *Tomenthyphum nitens*. In places, *Dicranum spadiceum*, *Racomitrium lanuginosum*, and *Rhytidium rugosum* can be abundant. The liverwort *Ptilidium ciliare* should also be mentioned among the dominants of the moss cover.

The mosses serve as an environment for many groups of organisms, both plants and animals. In this respect, the mosses in many ways determine the composition and structure of "zonal" communities. The total mass of living mosses is equal to, or even exceeds, that of the aboveground and belowground organs of flowering plants (Khodachek, 1969). Due to the dense moss turf on the "plakor" of typical tundras, there is a prevalence of long-rhizome vascular plants. The turf is inhabited by a rich complex of invertebrates, called hemiedaphon, which includes many species of springtails, mites, spiders, and rove beetles (Staphylinidae). At the same time, the moss cover is also inhabited by many soil animals; for example, earthworms, enchytraeids, larvae of craneflies, carabids, and others.

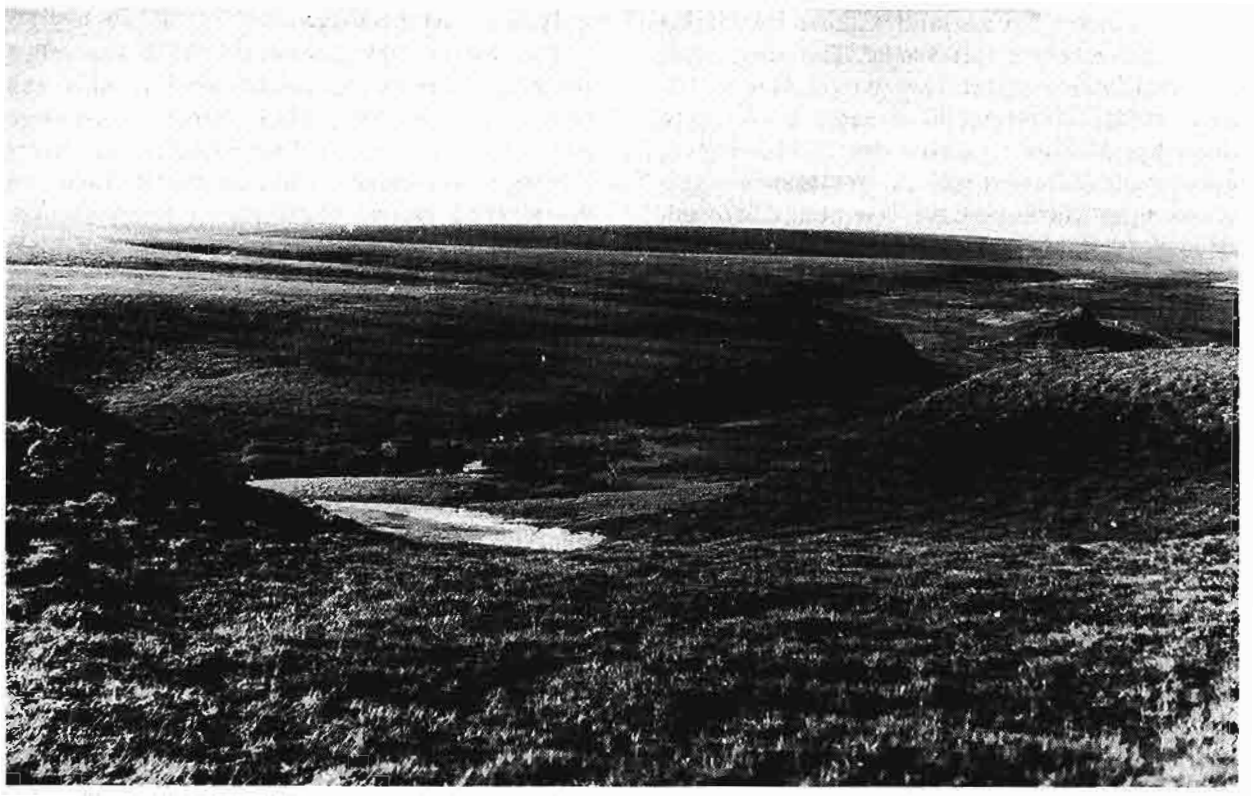


Fig. 16.16. Landscape of typical tundra at Tareya, Taymyr.

The field layer in the "zonal" communities of typical tundras is formed by sedges, such as *C. ensifolia* ssp. *arctisibirica*, *Carex globularis*, and *C. lugens*. There is a substantial proportion of some dwarf-shrubs, although they are not as abundant as further to the south. The main dwarf-shrubs in the typical tundra "zonal" communities are *Dryas octopetala* and *D. punctata*, as well as *Cassiope tetragona* and, less abundant, *Salix polaris*. The lichens are represented by fruticose and foliose forms and by practically the same species as in the southern tundra subzone.

The climatic conditions of the typical tundra subzone are not so extreme that the nontundra elements completely disappear from the biota; although their number does dramatically decrease. Especially rare are the boreal species, which are almost exclusively associated with "intrazonal" biotopes. Ericaceous dwarf-shrubs, which are so abundant further south, can still be found, but they are scarce and many of them rarely flower or their fruits do not ripen. Several species of Empetraceae, Geraniaceae, and Violaceae disappear totally, and the number of species in the large families Poaceae, Ranunculaceae, Rosaceae, Salicaceae, and Scrophulariaceae decrease.

In the animal world, the taxonomic impoverishment at the expense of boreal species is even more sharply pronounced. Already absent in the typical tundra are many birds which are common inhabitants of the southern tundra "zonal" landscapes – for instance, the lesser white-fronted goose (*Anser erythropus*), the stone plover (*Limosa lapponica*), and the eastern solitary snipe (*Gallinago stenura*). Among small mammals, only lemmings remain in most areas, whereas the voles, numerous to the south, are absent as a rule. Insectivorous mammals (Insectivora), terrestrial molluscs, gnats (Bibionidae), and leather-winged beetles (Cantharidae) become sporadic or disappear, although solitary specimens may penetrate far to the north. The diversity of Hemiptera sharply decreases and hypoarctic species also decrease markedly. The majority of them are still present with a few specimens in the southern part of the subzone, but disappear to the north. Only in some "intrazonal" communities on limited areas may the hypoarctic species be comparatively abundant. The main role in the

typical tundra communities is played by hemiarctic species. They are predominant in terms of the number of species in the biota and dominate in both the plant cover and the animal populations.

The impoverishment of the flora and fauna because of the disappearance of boreal forms is partly made up by the appearance of euarctic forms. However, in the typical tundra subzone, these forms are not yet as widely distributed as further north. On the whole, there is a kind of "purification" of the arctic biota, excluding species with more southerly distribution, while the total level of the species richness remains approximately the same.

A characteristic feature of the vertical structure of "zonal" communities of typical tundra is the low height of the whole profile (not more than 20 cm) and the short vertical distance occupied by each layer. The reduction in height of the shrub layer has a critical effect on the distribution of many species of animals. All the birds and insects directly associated with shrubs disappear from the "plakor" and migrate into the "intrazonal", mainly valley, communities. The sparse field layer cannot support concentrations of big insects. Therefore, the complex of inhabitants of the grassland becomes much impoverished. Anthophilous insects are also scarce because there are few entomophilous plants in the "plakor" tundras. Only on *Dryas* spp., during their period of mass blossoming, is there a large concentration of flies from the families Empididae, Muscidae, and Syrphidae.

The plant cover of "zonal" communities in the typical tundra can still be closed by the development of a moss turf, although frost-boil tundras occupy considerable areas. The mosaic structure of plant cover is typical for all communities on "plakor", due both to the growth form of the dominants and to the heterogeneity of the environment resulting from cryogenic processes in the soil.

A considerable decline in the role of many life forms (shrubs, dwarf-shrubs), the decrease in diversity of dominants, and the disappearance of strata and their compression all lead to a greater monotony in the landscapes of the typical tundra subzone than in the southern tundra. The communities on "plakor" are similar in their floristic composition, but differ physiognomically because of the varying abundance of the same species (subassociations or variants). In the "intrazonal" biotopes, however, one can find some types of communities which differ sharply from the "zonal" communities. The typical tundra "intrazonal" communities include a special type of mire, the polygonal mire. In the river valleys, there are thickets of low willows (*Salix lanata*), but more typical are moss carpets of *Bryum tortifolium* and *Calliergon giganteum* with a sparse cover of small flowering plants such as *Cardamine pratensis*, *Oxyria digyna*, *Ranunculus nivalis*, *R. sulphureus*, *Saxifraga cernua*, *S. hieracifolia*, and *S. hirculus*.

Dryas heaths on fell-fields without a moss cover are common within the typical tundra subzone. The vegetation, however, does not cover more than half of this community area. Colorful meadows are well developed on south-facing slopes, with a high abundance of the grasses *Festuca cryophila*, *Poa alpigena*, and *Trisetum sibiricum* and the herbs *Astragalus subpolaris*, *A. umbellatus*, *Cerastium maximum*, and *Pedicularis verticillata*. Typical in places with a long-lasting snow cover are communities with predominance of the dwarf-shrubs *Cassiope tetragona* and *Salix polaris*, the mosses *Drepanocladus uncinatus* and *Tomenthyphum nitens*, and the lichens *Cetraria cucullata*, *C. islandica* var. *polaris*, *Stereocaulon alpinum*, and *S. rivulorum*. Solitary specimens of *Ranunculus nivalis*, *R. pygmaeus*, *Saxifraga hyperborea*, and *S. tenuis* grow where snow does not melt until the middle of August.

Typical tundras in different sectors of the Russian Arctic have much in common both in the composition of biota and in the structure of the living cover, since the proportion of circumpolar species is greater than in the southern tundra. The similarity is also increased by the fact that this subzone is absent, or at least is not pronounced, at the extreme western and eastern limits of the tundras.

Arctic tundra subzone

On the mainland, this subzone is best developed on the Yamal, Gydan, and Taymyr, and in small fragments on the seashore from the river Anabar to the river Kolyma. Besides this, it is represented on the islands of the Arctic Ocean: Novaya Zemlya, Vaygach, Belyi, Novosibirskiye, and Vrangel. It occurs in the region of true arctic climate (the Arctic Belt of geographers). Its southern borders coincide approximately with the 4–5°C July isotherms, the northern limit with 1.5–2°C July isotherm. The climatic conditions of the subzone are extreme, exerting a strong negative influence on the biota and the structure of the cover (Fig.

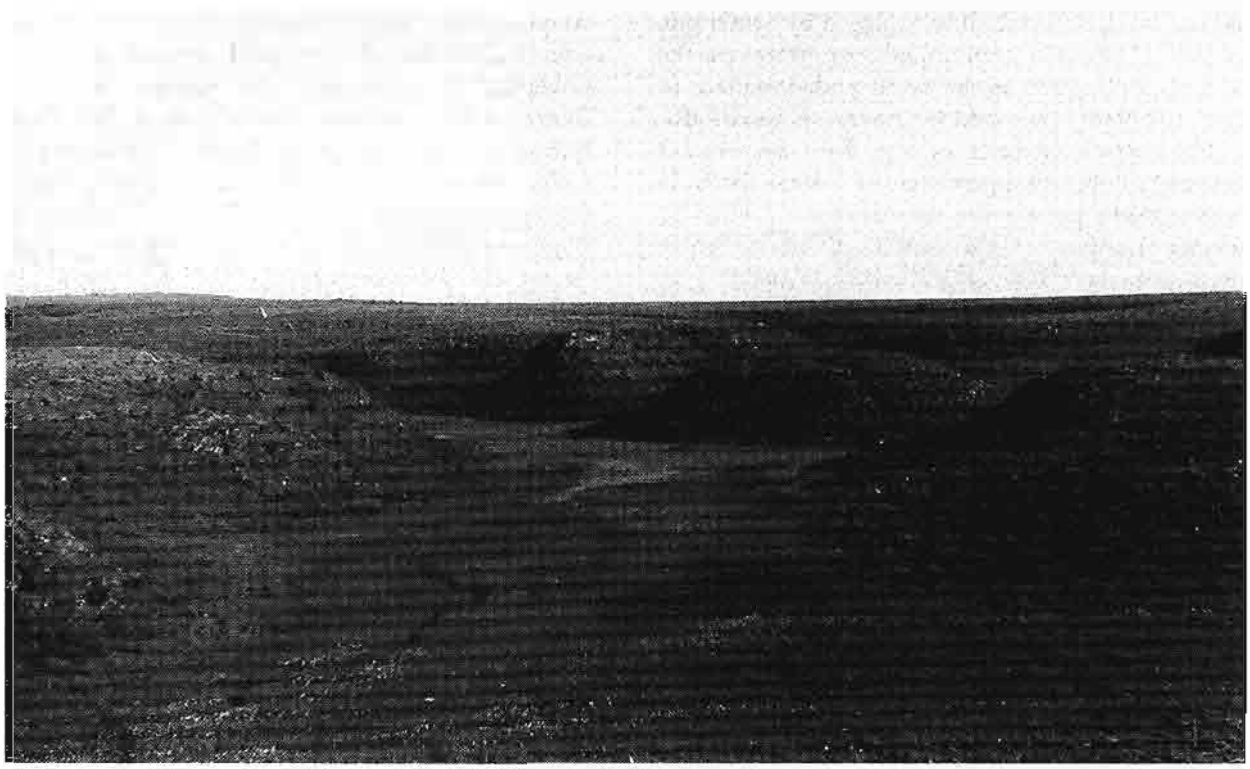


Fig. 16.17. Landscape of arctic tundra at Dikson, Taymyr

16.17). In the first place, this leads to a sharply reduced diversity of taxa at the species level and also at the genus and family levels. The impoverishment affects all groups of organisms, although to a different degree. It is most pronounced in the most advanced taxa (in more detail, see pp. 387–408). The number of species of flowering plants and of various groups of insects and soil invertebrates (among them spiders, beetles, and springtails) in the arctic tundra are reduced almost to half the figures for the typical tundra subzone. To a lesser degree, this is also observed for mosses and lichens and for birds and mammals. The arctic tundras are practically without any boreal and hypoarctic species, although some polyzonal organisms are still quite typical; for example, numerous mosses including the dominants, as well as lichens and soil algae. Some widespread birds and mammals can also still be found; for instance, the white wagtail (*Motacilla alba*), the common wheatear (*Oenanthe oenanthe*), and the ermine (*Mustela erminea*). A typical feature of the biota is a very high proportion of hemiarctic and euarctic species. The core of species which play the most important role in the "zonal" communities are mainly euarctic, including the plants *Alopecurus alpinus*, *Deshampsia borealis*, *Draba oblongata*, *D. subcapitata*, *Luzula confusa*, *Papaver polare*, *P. pulvinatum*, *Salix polaris*, *Saxifraga caespitosa*, and *S. hirculus* and the animals *Calidris testacea* (the red-breasted snipe), *Nyctea scandiaca*, (the snowy owl), *Plectrophenax nivalis* (the snow bunting), *Tipula carinifrons* (the cranefly) and *Tachinus arcticus*.

The structure of "zonal" communities changes as a result of missing or poor representation of some plant life forms which play a considerable role further to the south. The absence of shrubs and of almost all dwarf-shrubs results in the simplification of the vertical structure. The height of the profile decreases to 5 cm (the sparse flowering shoots reach 10 cm and in very rare cases up to 20 cm). The moss turf is 3–5 cm thick, with the major part of the vegetative shoots of the flowering plants being sunk into it. Stratification is almost nonexistent. The changes in the plant cover lead to a simplification of the vertical structure of animal population and a reduction of complexes of field-layer inhabitants, rhizophages, and inhabitants of deeper soil layers. The density of invertebrates is

highest on the soil surface, in the upper soil layer, and in the lower part of the moss turf. The role of various species groups in the structure of communities also changes. For example, the sedges and cotton grasses are replaced by grasses and forbs in "zonal" communities in the arctic tundra. In addition, many species change their growth form as compared to more southern regions: tufted grasses and herbs, cushions, and dense mats are formed and the number of vegetative shoots, often also that of flowering shoots, increases. The dwarf-shrubs are represented only by *Salix polaris*, which is fully submerged in the moss cover, with just the leaves lying on its surface. *Dryas* spp. do not grow any more in "zonal" communities on "plakor", but instead they inhabit the fell-fields. The liverwort *Ptilidium ciliare* disappears, while *Drepanocladus uncinatus* becomes abundant. The chief dominant mosses (*Aulacomnium turgidum*, *Hylocomium alaskanum*, *Tomenthypnum nitens*) retain their position. The bog mosses (*Sphagnum*) almost completely disappear from the plant cover. The abundance of the fruticose lichens *Cladina* and *Cladonia* is also dramatically reduced. At the same time, the role of the crustaceous lichens *Biatora*, *Lecidea*, *Ochrolechia*, *Pertusaria*, and *Rinodina* increases markedly.

The main feature of the structure of the plant cover of arctic tundras is a high proportion of bare ground on "plakor" (Figs. 16.18, 16.19). Here, the polygonal tundra, in which bare ground occupies 50% or more, predominates. Communities with closed cover are absent on "plakor". The successional processes going on in the "zonal" communities can no longer lead to a closed plant cover in this subzone. The vegetation fills in the cracks arising in the ground as a result of cryogenic processes. In consequence, the pattern of vegetation becomes netlike.

The general impoverishment of flora and the more uniform ecological conditions result in a decrease in the diversity of community types in the arctic tundras. "Zonal" communities are represented by few associations with similar composition, but with different patterns of cover.

One peculiarity of the arctic tundra subzone is the decrease in contrast between the tundra communities on well-drained, nearly flat areas and those in meadows on south-facing slopes. The latter are made up of the same species which grow in the "zonal" arctic tundra, namely *Alopecurus alpinus*, *Luzula confusa*, *Pedicularis sudetica*, *Poa alpigena*, *Saxifraga caespitosa*, and *S. hirculus*.

Fig. 16.18. Frost-boil community in the arctic tundra subzone at Dikson, Taymyr.

Mires are only developed in depressions. All the boreal sedges are absent and the arctic species *Carex stans* tends to be suppressed by the grass *Dupontia fisheri*. Also noticeable is the proportion of forbs (*Cardamine pratensis*, *Cerastium regelii*, *Chrysosplenium alternifolium*, *Saxifraga cernua*, *Senecio atropurpureus*) which are absent in the mires of the two southern subzones. In places of long-lasting snow cover, only solitary flowering plants will survive (e.g., *Ranunculus pygmaeus*, *Saxifraga hyperborea*, *S. tenuis*). Not infrequently, such areas are altogether devoid of plants, especially when the snow does not thaw annually.

As this subzone on the mainland of Eurasia is pronounced only in its center, the arctic tundras are very much alike in different regions. Nevertheless, the differences on the northern islands are in the composition of the biota rather than in the organization of communities.

Polar desert zone

The polar deserts lie north of the arctic tundra subzone. Genuine polar deserts are developed

Fig. 16.19. Polar desert with moss and lichen cracks in the ground at Cape Chelyuskin, Taymyr.

mostly on the northernmost islands: in the north of Novaya Zemlya, on Severnaya Zemlya, Zemlya Frantsa-Iosifa, the DeLonga islands, and, possibly, in the northernmost part of the Novosibirskiye islands. Polar desert exists only in one place on the mainland, on Cape Chelyuskin in Taymyr.

The organic world of polar deserts is very limited because of the extreme environment: low summer temperatures, small quantity of precipitation, inadequate thawing of permafrost, and a short growing period. Not only are elements of flora and fauna alien to the Arctic absent here, but also many arctic species. The vascular plant flora is most affected by this impoverishment. The number of species in local floras is reduced to 50, which is only half the number found in arctic tundra and one quarter of those in typical tundra. Even the diversity of mosses and lichens is reduced, although not as sharply. Nesting terrestrial birds are reduced to 2–3 species. Many of the animal groups important further south in the tundra have disappeared in the polar desert – for instance, earthworms, spiders, beetles, necrobiotic flies, sawflies, and others. Especially noteworthy is the absence of the cranefly *Tipula carinifrons*, the most characteristic arctic species of Tipulidae. The animal population in soils is mainly limited to only four groups of invertebrates: nematodes, enchytraeids, springtails, and larvae of chironomids. However, these are also depauperate taxonomically.

The major part of the ground surface in polar deserts is devoid of macrophyte cover. From 60 to 95% of the ground is bare. Vegetation fills in the narrow fissures between the polygons (Figs 16.19, 16.20), while elsewhere there are only a few solitary plants. Mosses and lichens dominate the plant cover, both in the number of species and in abundance. The main dominants in the communities of the tundra zone further south become less abundant, with the exception of *Aulacomnium turgidum* and *Racomitrium lanuginosum*. In the polar desert, the cryptogam cover is made up of the mosses *Bryum tortifolium*, *Dicranoweisia crispula*, *Ditrichum flexicaule* and *Orthothecium chryseum* and the lichens *Cetraria cucullata*, *C.*

Fig. 16.20. Polar desert with sparse plants distributed independently of the pattern of the cracks at Cape Chelyuskin, Taymyr.

delisei, *C. islandica* var. *polaris*, *Parmelia omphalodes*, *Stereocaulon rivulorum*, and *Thamnolia subuliformis*.

The flowering plants grow sparsely among the mossy strips or cushions, about a dozen species being most frequently found: *Alopecurus alpinus*, *Cerastium regelii*, *Deschampsia borealis*, *Draba oblongata*, *D. subcapitata*, *Eritrichium villosum*, *Papaver polare*, *Phippsia algida*, *Saxifraga cernua*, *S. foliolosa*, *S. hyperborea*, *S. oppositifolia*, and *Stellaria edwardsii*.

Denser communities are only formed in protected areas with sufficiently deep snow cover; for instance, *Potentilla hyparctica* on Zemlya Frantsa-Iosifa and *Senecio atropurpureus* on Severnaya Zemlya. Such areas are, however, a kind of oasis among the cryptogamic communities. In Eurasian polar deserts, flowering plants completely lose the leading role in the plant cover which they play in all other zones.

A typical feature of the vertical structure of communities of polar deserts is the absence of stratification. The moss cushions are not more than 5 cm thick; all other plants are either sunk into the moss or seem to lie on its surface. As the field layer is not pronounced, the whole complex of grassland invertebrates is absent. There are no typical anthophilous insects. Only a few species of beetle mites (Oribatei) and springtails are associated with flowers. The roots of the vascular plants are also concentrated in the moss turf or very close to the surface of the ground; only a few roots penetrate to a depth of 10–15 cm. Invertebrates are concentrated in the upper soil layer (0–2 cm). If the surface is even, then, even at a depth of 3 cm, there are no springtails or enchytraeids. The nematodes penetrate a little deeper, but they are also absent at a depth of 10 cm, or sometimes even at 5 cm.

The general poverty of the biota and the extreme environmental conditions cause those species which are adapted to polar desert conditions to occur everywhere. The dominating moss and lichen communities thus have very similar species composition all over the polar deserts. The abundance of species and their distribution depend on the size and shape of patterned grounds. A typical peculiarity of this zone is the disappearance of differences between "zonal" and "intrazonal" vegetation. In polar deserts, there are no herb–grass meadows on south-facing slopes nor snowbed communities. Mires are also absent.

The composition and structure of the organic world of polar deserts are extremely uniform in various regions of the Eurasian Arctic since circumpolar species are so important.

The main changes occurring in the composition and structure of the organic world in high latitudes from the forest border to the polar deserts are thus the progressive impoverishment of biota, a reduction in all indices of mass and abundance, a vertical compression of strata, and the reduction in plant cover.

THE COMPOSITION OF THE ARCTIC BIOTA

All forms of diversity in the tundra zone – qualitative composition, community diversity, adaptive types, life forms, functional groups – are diminished in comparison with the biomes at more southerly latitudes. When characterizing the tundra communities it is, therefore, very important to record what they consist of and what they are lacking. This is necessary in order to understand the functioning and the stability mechanisms in arctic ecosystems.

Low taxonomic diversity in plant and animal populations of the tundra zone leads to a poor ecological vicariance – to a low interchangeability of species performing certain functions in communities. In the northern tundra landscapes, there is often only a single-species representation of many large systematic groups playing a particular ecological role (Chernov, 1978b). Therefore, diversity is of great significance in the communities of the

TABLE 16.4

Role[1] of some vascular plant groups in the Taymyr plant communities[2]

Plant group	Southern tundra	Typical tundra	Arctic tundra	Polar desert
Liliopsida (Monocotyledones)				
Poaceae	++	++	++++	+++
Cyperaceae	+++	++++	+	–
Juncaceae	+	+	++++	–
Magnoliopsida (Dicotyledones)				
Salicaceae (shrubs)	++++	+++	–	–
Salicaceae (dwarf-shrubs)	++	++	++++	–
Betula spp.	++++	++	–	–
Caryophyllaceae	+	+	+	+++
Papaveraceae	+	+	+++	+++
Brassicaceae	+	+	+++	+
Saxifragaceae	+	+	++++	+++
Rosaceae	+++	++++	++	–
Fabaceae	++	++	+	–
Ericaceae	++++	+++	–	–
Scrophulariaceae	+	++	+	–
Asteraceae	+	++	+	–

[1]++++, widely distributed species, dominants in the "zonal" communities; +++, frequent, but not abundant in the "zonal" communities; ++, infrequent, but sometimes abundant in "intrazonal" communities; +, rare species with low abundance; –, very rare or absent.
[2]From Chernov and Matveyeva (1979).

tundra zone. The well-known principle of the ecological uniqueness of each species and of the negative consequence of withdrawal of any of them from an ecosystem can be particularly applicable to the arctic biomes.

The incompleteness of the tundra biota finds its expression in the absence of many large taxa, the decrease in species diversity, as well as the reduction of the number of ecological forms and adaptive types which, as a whole, lead to a qualitative impoverishment of the various functional elements of the ecosystems. All of this intensifies the fragility and instability of tundra communities.

Character and causes of impoverishment of the arctic biota

The northern tree line is a clear-cut ecological border limiting the northward distribution of many groups of organisms. Thus, important components of forest communities, such as conifers, ferns, most macrofungi, amphibians, diplopods, and terrestrial molluscs, disappear in the tundra. Other large groups that are very important and diverse in the boreal forests are represented in the tundra by single, although sometimes widespread, species, such as *Pachypleurum alpinum* in the Apiaceae and *Monotarsobius alticus* in the Chilopoda. Other taxa are well represented in the southern part of the tundra zone, but are very rare at high latitudes. Species of Ericales are, for instance, important components of the flora and vegetation both in the taiga and in the southern tundra, while in the middle of the tundra zone their significance in the plant cover and their species number decrease sharply, and they are practically absent in the arctic tundra subzone. The process of impoverishment in various groups of organisms at high latitudes varies and depends on different factors (Tables 16.4, 16.5).

The ratio of the number of species, life forms, trophic groups, etc., between the tundra and the boreal flora and fauna is between one-quarter and one-third. There are more than 1500 vascular plants in the district around St. Petersburg, 1052

TABLE 16.5

Diversity[1] of the orders of insects in the polar regions[2]

Order	Forest tundra	Southern tundra	Typical tundra	Arctic tundra	Polar desert
Collembola	+++	+++	+++	+++	+++
Ephemeroptera	+++	++	++	–	–
Odonatoptera	+	+	–	–	–
Orthoptera	++	–	–	–	–
Plecoptera	+++	+++	+++	++	+
Dermaptera	+	–	–	–	–
Psocoptera	++	–	–	–	–
Homoptera	+++	++	+	–	–
Hemiptera	++	++	+	+	–
Thysanoptera	++	++	+	–	–
Coleoptera	+++	+++	+++	+++	+
Megaloptera	+	+	+	–	–
Neuroptera	+	–	–	–	–
Mecoptera	+	–	–	–	–
Trichoptera	+++	+++	+++	+	–
Lepidoptera	+++	+++	+++	++	+
Hymenoptera	+++	+++	+++	++	+
Diptera	+++	+++	+++	+++	+++

[1]+++, many species and adaptive types with significant cenotic role; ++, a few species with a significant cenotic role; +, single species with negligible cenotic role.
[2]From Chernov (1978b).

TABLE 16.6

Species numbers in the subgenera of *Tipula*[1]

	Total number of species in			
	World fauna	Palaearctic fauna	Boreal fauna of Eurasia	Tundra fauna of Eurasia
Angarotipula	4	4	2	1
Arctotipula	23	12	8	4
Beringotipula	15	1	1	1
Lunatipula	310	167	37	3
Odonatisca	8	5	3	2
Oreomyza	?	35	12	3
Platytipula	63	35	4	1
Pterelachisus	70	56	23	7
Savtshenkia	50	37	27	6
Vestiplex	114	70	13	7
Yamatotipula	84	49	18	4
Total	> 741	471	148	39

[1]From Lantsov and Chernov (1987).

species in the Kola peninsula (Ramenskaya, 1983), but only 475 species in the Bol'shezemel'skaya Tundra (Rebristaya, 1977), about 415 species in Taymyr, and 592 species in the mountain regions of northeastern Asia on the Anyuyskoe plateau (Zaslavskaya, 1982). One of the most important families of Diptera in the arctic fauna is the Tipulidae. This family has about 170 species in boreal regions, whereas there are only about 50 species in the Eurasian tundra (Savchenko, 1969, 1983; Lantsov and Chernov, 1987). The ground beetles, Carabidae, are represented by six life forms in the tundra zone and by 17 forms in the taiga of the European part of Russia (Sharova, 1981). Almost the same relationship is observed for smaller taxa: a good example for this is the main genus of the Tipulidae, *Tipula* (Table 16.6). The scale of impoverishment of flora and fauna in the tundra zone can be well seen if one takes into consideration the entire territory of the former Soviet Union, including practically the entire system of the temperate and cold belts of Eurasia (Tables 16.7, 16.8).

Nevertheless, the reduced species number in the tundra zone as a whole does not fully explain the character and the scale of the reduction in the organic world of the extreme arctic. The main feature of the composition is an increasing poverty in the number of species from south to north in the tundra zone (Table 16.9). The number of species in most of the larger animal and plant groups falls to zero or to very few species from the southern border of the tundra to the extreme north. The

TABLE 16.7

Number of species of avifauna (excluding marine groups) in the Eurasian tundra zone[1]

Order	Occurring only, or mainly, in the tundra zone		Distributed in the tundra and adjacent zones	Invading the tundra zone from the			Total species number in the tundra zone	Tundra spp. percent of total species number in the former Soviet Union
	In the entire territory	Locally		South	Mountains	Arctic basin		
Gaviiformes	2	1	1	0	0	0	4	100.0
Anseriformes	6	7	2	6	1	2	24	45.2
Falconiformes	2	0	1	2	0	0	5	10.2
Galliformes	1	0	1	0	0	0	2	9.5
Gruiformes	0	1	0	2	0	0	3	13.0
Charadriiformes								
Limicola	11	10	2	4	2	3	32	43.2
Larus	5	2	1	2	0	1	11	32.3
Strigiformes	1	0	0	1	0	0	2	11.1
Passeriformes	4	0	3	14	1	0	22	6.6
Total	32	21	11	31	4	6	105	15.5

[1]Data on the tundra zone from Danilov (1966) with some changes; data on the fauna of Russia as a whole from Stepanyan (1975, 1978, 1983).

TABLE 16.8

Number of terrestrial species of mammals in the tundra zone of Eurasia[1]

Order	Occurring only, or mainly, in the tundra zone	Distributed in the tundra and adjacent zones	Invading the tundra from adjacent zones	Total species number in the tundra zone	Tundra spp. percent of total species numbers in the former Soviet Union
Artiodactyla	0	1	2	3	13.6
Carnivora	1	3	5	9	20.5
Insectivora	0	1	4	5	13.2
Lagomorpha	0	1	1	2	16.7
Rodentia	4	1	11	16	12.1
Total	5	7	23	35	12.2

[1]From Shwarts (1963).

diversity of life changes much more within the tundra than in the area from the deciduous (broad-leaved) forests (which is the richest biome in the temperate belt) to the tundra. This is a consequence of very sharp environment gradients, and, first and foremost, of the summer temperature.

The tree line, which determines changes in the cenotic significance of various groups of organisms is, however, not an insurmountable biogeographic (floristic and faunistic) "barrier". Many plant and animal groups penetrate far into the tundra, although their role in tundra ecosystems becomes far less significant than in the forests. Most frequently, such species inhabit only southern tundra landscapes, although a few of them, using certain biotopes, spread up to the arctic tundra or even to the polar desert. Some boreal ericoids are a good example of such distribution with increasing impoverishment in the tundra zone (Table 16.10).

Among the animals, the same picture is given by the Insectivora. The members of this order are prominent components of the biocenoses in forest communities up to the open woodlands and forest tundra. It is mainly represented there by the shrew family (Soricidae), which in the forest occupies the ecological niche of consumers of soil and litter invertebrates. These animals do not go into hibernation, so that the environment during the winter period (snow depth, degree of soil freezing) is of great significance. Some authors consider the shrews as common and cenotically important inhabitants of the tundra, but that is hardly correct.

TABLE 16.9

Species number[1] of different taxa in the local Taymyr flora and fauna[2]

	Southern tundra subzone (Kresty)	Typical tundra subzone (Tareya)	Arctic tundra subzone (Maria Pronchishcheva Bay)	Polar desert (Cape Chelyuskin)
Vascular plants	241	239	96	57
Spiders	–	19	9	2
Springtails	96	62	29	12
Bugs	12	4	1	0
Beetles	68	35	9	2
Birds	50	47	32	9
Mammals	15	8	6	3

[1]Species number in sites where detailed research has been carried out. The term "local flora (fauna)" is used here as a conditional equivalent to the concept of "concrete flora (fauna)" according to Tolmachev (1986). We consider local flora (fauna) as a set of species that occur on a minimal area which includes the most characteristic habitats for certain climatic conditions in the zone or subzone in question. In the Arctic, this area does not exceed 10 × 10 km – that is, the territory that can be easily studied during a relatively short time.
[2]From Chernov (1978b, 1985).

The tundra environment is quite unfavorable for these animals. There is no soft leaf litter, the snow cover is too dense, and the moss turf is frozen. That is why they are very common only in the southern tundra and in forest tundra where the litter inhabited by invertebrates accumulates under shrubs. There are five species of *Sorex* (*S. araneus*, *S. daphaenodon*, *S. minutissimus*, *S. minutus*, and *S. tundrensis*, plus *Neomys fodiens* which occur mainly in the forest tundra, but also to some extent in the southern tundra (Shwarts, 1963). Only *S. tundrensis* reaches the typical tundra subzone, while the other species are restricted in their northward distribution to the forest tundra or the very southern part of the tundra. Thus, as a whole, this group is not able to occupy tundra landscapes, although a few species can reach far to the north into the Arctic.

Sometimes the distribution of a large taxonomic group can be sharply limited by the southern tundra border. For instance, amphibians are not, as a rule, found north of the forest tundra. The species *Hynobius keyserlingi*, *Rana amurensis*, *R. temporaria*, and *R. terrestris* are often recorded in different parts of the forest tundra. Among them, *Hynobius keyserlingi* shows the closest correlation between its distribution limits and the northern limits of coniferous species, which is well seen in Yakutiya (Borkin et al., 1984). However, in northeastern Asia, this species penetrates into the southern tundra as does *Rana terrestris* in Yamal. The reduction of insectivorous species in the tundra ecosystems is due to various ecological factors, both biotic and abiotic, although the reasons for the zonal limits in their distribution are rather vague. In the case of amphibians, however, they are clearer: the summer temperature limits their development.

The main factor for the qualitative impoverishment of the tundra communities is the lack of heat, although it does not exert direct influence in every particular case. Much more frequently, reduced species diversity results from the restricted food supply or the lack of certain substances, such as nitrogen, as a result of the lower temperatures.

The most cardinal changes in the composition of communities are related to the absence of trees. There are many dendrophilous organisms connected with the crowns, wood, roots, and litter, that are absent in the tundra zone. The largest "losses" are among the fungi and insects. One of the most important components of the forest eco-

TABLE 16.10

Distribution of ericaceous species on Taymyr[1,2]

Species	Forest tundra	Southern tundra		Typical tundra		Arctic tundra	
	Noril'sk	Forest islet Ary-Mas	Kresty	Tareya	Rogozinka River	Dikson	Maria Pronchishcheva Bay
Andromeda polifolia	++	++	+	+	–	–	–
Arctostaphylos alpina	+++	+++	++	–	–	–	–
Cassiope tetragona	+++	+++	+++	++++	+	–	–
Chamaedaphne calyculata	+++	+	–	–	–	–	–
Empetrum subholarcticum	+++	+++	+++	–	–	–	–
Ledum palustre s.l.	+++	+++	+++	++	–	–	–
Moneses uniflora	+	–	–	–	–	–	–
Orthilia obtusata	++	++	+	+	+	–	–
Oxycoccus microcarpus	++	+	–	–	–	–	–
Pyrola minor	+	–	–	–	–	–	–
P. rotundifolia	+++	+++	+++	+++	++	+	–
Vaccinium myrtillus	+	–	–	–	–	–	–
V. uliginosum s.l.	++++	+++	++++	++	++	+	–
V. vitis-idaea s.l.	+++	+++	+++	+++	++	+	–
Number of species	14	11	9	7	5	3	0

[1]From Moskalenko (1970); Polozova and Tikhomirov (1971); Vargina (1978); Matveyeva (1979b); Safronova (1979); Kozhevnikov (1986); Matveyeva and Zanokha (1986); and authors' unpublished data.
[2]Explanations of symbols as in Table 16.4.

systems is the litter, which is inhabited by specific organisms forming the trophic chains of decomposition. Such litter is not characteristic of tundra communities. It is accumulated in small amounts in shrub communities in the southern tundra subzone, and there it is inhabited by some saprophages typical of the forests, such as Bibionidae. Their larvae actively destroy the leaf litter (Striganova and Chernov, 1981). Active saprophagous Diplopoda do not penetrate into the tundra zone, being episodic only near its southern limit and in the forest tundra, for instance *Pterroiulu fuscus*.

There is a substrate in the tundra zone that can be compared with the forest or steppe litter; that is, the plant material cut off by small mammals, often called lemming "hay". These accumulations of plant remains are inhabited by various small saprophilous invertebrates, such as springtails, mites, enchytraeids, and nematodes. Specialized forest-litter saprophages are, however, absent from lemming "hay" due to the ephemeral nature and sporadic distribution of this specific substrate.

The brevity of warm periods is one of the most negative factors for life in polar regions. Nevertheless, some animals, such as springtails, are able to live actively and to use the solar radiation when there is snow cover. Winter is also the best time for lemming breeding.

The shortness of the polar summer creates great difficulties for the breeding of many birds, particularly large species. Large birds such as the peregrine falcon (*Falco peregrinus*), snowy owl (*Nyctea scandiaca*), and various geese hardly have time to complete their breeding cycle in the tundra. They start to nest when there is still snow and air temperatures are negative. About 75 days are necessary for the full breeding cycle (from egg laying to the fledging of the young) in the large geese (*Anser albifrons*, *A. fabalis*, *Chen hyperboreus* (Syroechkovskyi, 1978). Thus, if they finish laying eggs in the middle of June, their young are not ready to fly before early September, which is when the birds must leave the tundra. Therefore, geese here are barely able to complete their cycle, even though they are well adapted to the environments. The smallest of the swans, *Cygnus bewickii*, needs even a little more time for nesting and the development of its nestlings. Therefore, this species cannot live north of the typical tundra subzone. As many as 160–180 days are necessary for the full breeding cycle of the largest swans, *C. cygnus* and *C. olor*. In order to survive in the tundra they would have to begin to lay eggs in the middle of April, which is quite impossible in the "zonal" Siberian tundra landscapes. Thus, the brevity of the growing season causes critical difficulties for the breeding of geese and absolutely prevents life in the tundra for large swans. The shortness of the tundra summer is not of great ecological significance for numerous small species, such as those of the suborder Charadrii and passerine birds, whose breeding cycle is only about 30 days. For example, if the Lapland bunting (*Calcarius lapponicus*) lays eggs at the beginning of July, the nestlings will grow and become independent by the middle of August when it is still warm and food is abundantly available.

Many boreal species widely spread in the forest belts are found far into the tundra zone. A considerable number of them find favorable conditions in the southern tundra subzone. It is not infrequent for some multizonal or boreal species to have a maximum population density just in the Subarctic. Ducks are a good example of this. In the southern tundra subzone, the river ducks of the subfamily Anatinae (*Anas acuta*, *A. clypeata*, *A. crecca*, *A. penelope*) are absolutely predominant. In the arctic tundra subzone, however, they are completely replaced by the so-called sea, or diving, ducks (subfamily Aythynae) with typical representatives of the arctic avifauna including *Clangula hyemalis*, *Somateria fisheri*, *S. spectabilis*, and *S. stelleri*. Another example is the bluethroat (*Luscinia svecica*), which is widespread in the forest belt but is very sporadic and not abundant in the main part of the distribution area. It becomes very common and abundant in the forest tundra and in the southern tundra. The role of *Alnaster fruticosus* and *Eriophorum vaginatum* in the "zonal" plant communities in the southern tundra subzone is also much more important than in the forest belt.

Thus, the distribution limits of various groups and species at the border between forest and tundra are determined by various biotic and abiotic factors, which have an unequal influence on different organisms. Their distribution also depends on the regional climatic and landscape conditions.

The zonal borders do not strictly coincide with particular latitudes – for instance, the southern border of the tundra zone in northeastern Europe runs along 67°N, while in Taymyr the border is at about 70°N. This reflects essential distinctions between certain climatic elements in the different regions. The proportion of typical arctic species is

greatest in the Taymyr. Its flora and fauna are more "arctic" than in analogous "zonal" landscapes of other parts of the tundra zone. For example, the proportion of arctic species (excluding hypoarctic) among vascular plants reaches 66% in the typical tundra subzone in the Taymyr, 59% in the Bol'shezemel'skaya Tundra, and 45–55% in Chukotka (Polozova and Tikhomirov, 1971; Rebristaya, 1977; Zaslavskaya, 1982).

The number of species of vascular plants in the southern tundra subzone of northern Europe is much greater than that in the typical tundra subzone, whereas in the southern and typical tundras in Taymyr this value is approximately the same (Table 16.11). The local floras in the southern tundra subzone are richer in the European region than in Taymyr. The explanation of these distinctions is as follows. Many boreal and multizonal species are more numerous in the tundra zone in northern Europe, while their numbers decrease sharply in the typical tundra subzone. On the other hand, the total number of typical arctic species is smaller in the European region, because many of them have the western limit of their distribution area in Taymyr, Gydan, or polar Ural. The similarity in the number of species in the local floras in the southern and typical tundras of the Taymyr is due to the less intensive expansion of southern elements because of the more severe climate.

Birds show a somewhat different picture (Table 16.12). The number of species in the local avifaunas in each subzone of these two regions, is almost equal in spite of essential differences in the landscape structure and development of the fauna. This is because the number of bird species depends rigidly on the summer heat conditions, which are uniform in a given subzone.

TABLE 16.11

Number of vascular plant species in the local floras of two tundra zone regions[1]

Subzone	Bol'shezemel'skaya tundra	Taymyr
Typical	193	239
Southern	283	241

[1]From Polozova and Tikhomirov (1971), Rebristaya (1977), and Matveyeva and Zanokha (1986).

Arctic and nonarctic species

The penetration of the southern species into the tundra zone adds noticeably to the poor arctic biota, much more than the addition of High Arctic species in the north of the tundra. True arctic species generally do not predominate in the local faunas and floras except in the arctic tundra subzone and polar deserts. For example, there are about 35 mammals in the Eurasian tundra (Table 16.8), but only 5 of them, distributed mainly in the tundra zone, can be considered as truly arctic species. There are only 8 arctic species among 30 syrphids found in the northern part of the tundra zone (Chernov, 1978b). It is natural that the overwhelming numbers of nontundra species are distributed mainly in the southern parts of the Arctic, where many of them play a significant role in the communities, especially in the "intrazonal" communities.

Although southern elements disappear from the vascular flora and the vertebrate fauna at the highest latitudes (in the arctic tundra subzone and in the polar desert), this does not apply to the whole biota. Microorganisms and some more primitive groups (Fungi, Algae, Protozoa, Nematoda, Bryophyta) are represented mainly by widespread, multizonal, and even cosmopolitan species. Many large groups that are widely distributed in the tundra zone have no typical arctic species. No such species have, for instance, been found among yeasts; only a few of them show a tendency to be more abundant under tundra conditions (I. Chernov, 1985). There are practically no tundra species among soil algae (Sdobnikova, 1986). Only a very few bryophytes can be considered as arctic species, and all common and dominant species are

TABLE 16.12

Number of bird species in the local faunas of two tundra zone regions[1]

Subzone	Bol'shezemel'skaya Tundra and Vaygach	Taymyr
Arctic	36	37
Typical	47	47
Southern	64	56
Forest tundra	70	70

[1]From Krechmar (1966), Uspenskyi (1969), Vinokurov (1971), Vronskyi (1987) and Tomkovich and Vronskyi (1988).

TABLE 16.13

Number of species in the Taymyr local floras[1]

Plant group	Southern tundra		Typical tundra	Arctic tundra		Polar desert
	Ary-Mas	Kresty	Tareya	Dikson	Maria Pronchishcheva Bay	Cape Chelyuskin
Vascular plants	256	241	239	134	96	57
Mosses	140	156[2]	175	130[2]	65[3]	74
Liverworts	48	53	46	78	46	25
Lichens	210	240[2]	117[2]	–[4]	180[2]	160[2]
Soil algae	–	238	157	131	–[4]	100

[1]From Piin and Trass (1971), Polozova and Tikhomirov (1971), Blagodatskikh (1973), Dorogostaiskaya and Sdobnikova (1973), Zhukova (1973, 1978, 1986), Afonina (1978), Martin and Piin (1978), Vargina (1978), Blagodatskikh et al. (1979a,b), Matveyeva (1979b), Piin (1979a,b, 1984), Safronova (1979), Kannukene and Matveyeva (1986), Matveyeva and Zanokha (1986), Sdobnikova (1986), and unpublished data by the authors.
[2]Including taxa which have not been determined as exact species, because of taxonomic difficulties.
[3]Incomplete data.
[4]–, no data.

multizonal. There is also a very high proportion of multizonal (including cosmopolitan) species among lichens (Piin, 1984).

Composition of taxa of the biota

The structure of the tundra biota, the level of species diversity, etc., differ sharply from those of the boreal flora and fauna. All taxa in the tundra are poorer in composition than in the boreal belt, but the impoverishment is not the same in different taxa.

Mammals are a good example of more or less uniform northward reduction in species diversity in all orders (Table 16.8). In each of the main orders, 15–20% of the total fauna of the former Soviet Union are found in the tundra zone. Bats (Chiroptera) are absent in the tundra and are not typical for the taiga, as only a few species get into its southernmost parts. Birds, on the other hand, give another picture (Table 16.7). The number of orders is reduced to half those in the boreal avifauna. In the tundra, there are for instance no grebes (Podicepediformes), stork-like birds (Ciconiiformes), cuckoos (Cuculiformes), pigeons (Columbiformes), or woodpeckers (Piciformes). The representation of other bird orders in the tundra varies from 6 to 100% of the total number of species in the former Soviet Union. The unevenness of the taxonomic impoverishment of the

TABLE 16.14

Number of species in the main families of vascular plants on Taymyr[1]

Family	Southern tundra (Kresty)	Typical tundra (Tareya)	Arctic tundra (Maria Pronchishcheva Bay)	Polar desert (Cape Chelyuskin)
Liliopsida (Monocotyledones)				
Poaceae	32	30	15	8
Cyperaceae	19	24	5	2
Magnoliopsida (Dicotyledones)				
Ranunculaceae	16	15	7	4
Saxifragaceae	10	13	14	10
Caryophyllaceae	21	20	11	6
Brassicaceae	13	25	16	8
Asteraceae	20	22	4	2

[1]From Polozova and Tikhomirov (1971), Matveyeva (1979b), Safronova (1979) and Matveyeva and Zanokha (1986).

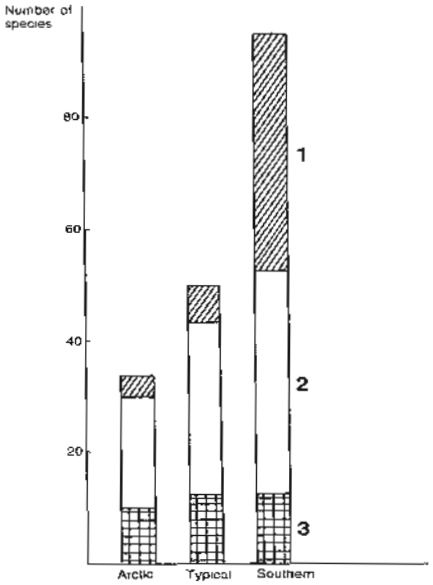


Fig. 16.21. The number of species of tipuloid dipterans (Tipuloidea) in different subzones of the tundra zone. 1, Limoniidae; 2, Tipulidae; 3, Trichoceridae. From Lantsov and Chernov (1987).

various groups of organisms, as the environment becomes more severe, is one of the main laws of transformation of the biota. A sharp reduction in one group is compensated by increments in others. It is especially obvious when analyzing the changes in species composition in the subzones (Tables 16.13–16.15; Figs. 16.21, 16.22). The decrease in the species number in the local floras of Taymyr is not the same in three main plant groups (Table 16.13). From the southern tundra subzone to the polar desert, the species number of vascular plants is reduced by about 75%, that of mosses by 50%, and that of lichens by about 30%. The strong reaction of vascular plants to the increased harshness of the environment compared to that of mosses and lichens can be explained by the level of their evolutionary development.

The species diversity of most vascular plant families is very similar in the southern and typical tundra subzones, but is sharply reduced in the arctic tundra subzone, and especially in the polar desert (Table 16.14). The number of *Saxifraga* species, however, becomes greater at high latitudes. This genus demonstrates a kind of biological activity in the tundra, a type of wide adaptive radiation. There are typical mesophilous plants amoung them (*Saxifraga caespitosa, S. hieracifolia, S. nelsoniana*), but also xeromorphic species (*S. flagellaris, S. spinulosa*). *Saxifraga oppositifolia* is a mesophilous herb with soft leaves in the typical tundra subzone and a xeromorphic semi-dwarf-shrub with sclerophyllous leaves in the polar desert. There are *Saxifraga* species in the arctic tundra subzone that grow in meadows on southern slopes (*S. hieracifolia, S. nelsoniana*), in fell-fields (*S. oppositifolia*), in snowbeds (*S. nivalis, S. rivularis, S. tenuis*), in wet mires (*S. foliolosa*), in patches of bare ground (*S. cernua, S. platysepala*), and in moss turfs in "zonal" communities (*S. caespitosa, S. hirculus, S. spinulosa*). There is no other landscape where *Saxifraga* species are of such significance in the plant communities. Some of them remain active even in the polar desert (*S. cernua, S. oppositifolia, S. rivularis*). Thus, this group does not show any signs of decreased diversity when the climatic conditions become extreme.

One of the most striking features of tundra flora and vegetation is the high proportion of monocotyledons. They total an average of about 30% of the arctic vascular plant flora — Eurasian polar desert: 30% (Aleksandrova, 1983); Canadian arctic archipelago: 47.6% (Porsild, 1957); Alaskan arctic slope: 27% (Wiggins and Thomas, 1962); Vrangel Island: 34% (Petrovskyi, 1978); Bol'shezemel'skaya Tundra: 29% (Rebristaya, 1977); Anyuyskoe plateau: 28% (Zaslavskaya, 1982); Taymyr arctic tundra subzone: 25%;

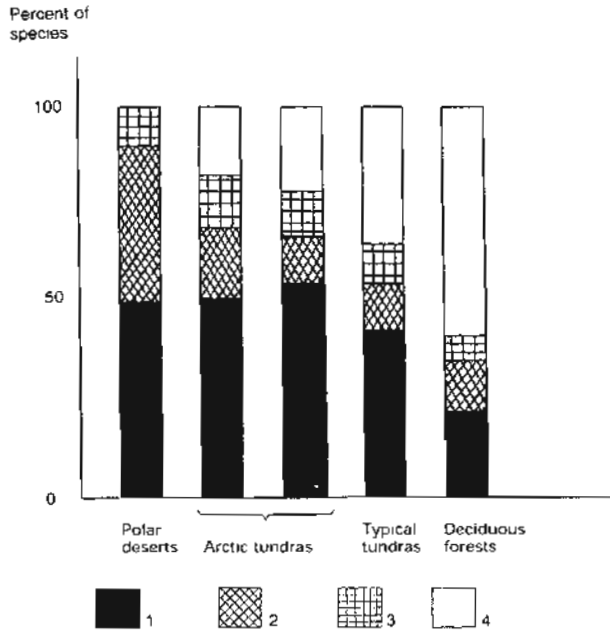


Fig. 16.22. Changes in the proportion of Collembola families from polar desert down to the deciduous forests. 1, Isotomidae; 2, Hypogastruridae; 3, Onychiuridae; 4, other families. From Ananjeva et al. (1987).

Taymyr typical tundra subzone: 26.8%; Taymyr southern tundra subzone: 26.1%; Taymyr polar desert: 22.8% (Polozova and Tikhomirov, 1971; Matveyeva, 1979b; Safronova, 1979; Matveyeva and Zanokha, 1986).

The largest and most advanced family of dicotyledons, Asteraceae, plays a very small role in the arctic flora and vegetation compared to more southerly areas. For instance, in the Taymyr, this family totals 8–9% of all vascular plants in southern and typical tundras and only 3–4% in arctic tundra and polar desert. There are only 4 species of Asteraceae in the whole of the Eurasian polar deserts (Aleksandrova, 1983). All of them are distributed very locally and have very low abundance.

The species number of geese-like birds (Anseriformes) and passerine birds (Passeriformes) is reduced to about half in the arctic tundra subzone and by 80–90% in the polar desert, when compared to the southern tundra subzone (Table 16.15). However, the species number of Charadriiformes (Lari and Charadrii) does not decrease, but even increases in the typical tundra subzone compared to further south and remains at the same level in the arctic tundra subzone.

Passerine birds are primarily forest birds, but their diversity in the steppe and the desert is also relatively high. Tundra is the only "zonal" landscape where passerine birds do not play their usual leading role. Only four species can be considered typical for the Eurasian tundra landscapes: Lapland bunting (*Calcarius lapponicus*), snow bunting (*Plectrophenax nivalis*), shore lark (*Eremophila alpestris*), and red-throated pipit (*Anthus cervinus*). Nevertheless, *A. cervinus* is mainly located in the southern tundra subzone and in the forest tundra, *P. nivalis* is an inhabitant of local "intrazonal" biotopes, and *E. alpestris* is an arctic–alpine species that chooses the driest and most elevated places. Only *C. lapponicus* is a typical representative of the "plakor" tundra communities; it is the only real tundra species in both the geographical and the ecological sense.

Passerine birds vacate most of the diverse ecological niches in tundra communities. These niches are occupied by the Charadriiformes (sandpipers, plovers, seagulls, skuas), which have proved more adaptable to the polar conditions – specifically to more hydrophilous environments.

Many features that passerine birds have in the forest landscapes are very characteristic for Charadriiformes in the tundra zone — for instance, a wide adaptive radiation, a diversity of life forms and ethology, and a high population density. Thus, there are many small entomophages among tundra sandpipers and plovers which nest with high density (comparable with the density of passerine birds in the forests) and feed on free-flying insects or on those living in the grass stands or moss turf. Medium-sized, very polytrophic species are inclined to be phytophages: ruff (*Philomachus pugnax*), the black-bellied plover (*Pluvialis dominica*), and the lesser golden plover (*P. squatorola*), which are all vicarious for the thrushes (*Turdus*) of great importance further south. Various seagulls (*Larus*) and skuas (*Stercorarius*) are typical polytrophic birds inclined to be necrophagous species, predators, or species associated with man, and can be considered as the ecological analogue of crows.

TABLE 16.15

The number of species of nesting birds in Taymyr tundra subzones[1]

Order	Forest tundra	Southern tundra	Typical tundra	Arctic tundra	Polar desert	Total
Anseriformes	14	9	7	5	1	16
Charadriiformes	14	18	23	16	6	35
Falconiformes	3	2	2	1	–	4
Galliformes	2	1	2	1	–	3
Gaviiformes	3	3	3	2	–[2]	3
Passeriformes	18	10	9	6	2	20
Strigiformes	1	1	1	1	–	2
Total	55	44	47	32	9	83

[1]From Krechmar (1966), Vinokurov (1971), Chernov (1978b), with additions.
[2]No data available.

There are many reasons for the sharp reduction in the proportion of passerine birds and for the increase of the Charadriiformes in the tundra zone. One reason may be the different levels of evolutionary development of these groups, a question which will be discussed later. More concrete reasons should, however, also be taken into consideration; for example, the manner of life, the physical features, etc. Passerine birds probably cannot, in principle, extract invertebrates from the tundra soil and moss turf, a feat which many species of the Charadrii can do because of their peculiar bill construction (its innervation).

The most striking feature of the arctic entomofauna is a low proportion of insects with incomplete metamorphosis (Hemimetabola), such as Heteroptera, Homoptera, Orthoptera, and Thysanoptera, and an absolute domination of orders with complete metamorphosis (Holometabola) such as Coleoptera, Diptera, Hymenoptera, Lepidoptera, and Trichoptera (Chernov, 1978b, 1984a). This phenomenon is the consequence of the tundra climatic conditions, the first and foremost being the lack of heat. Incomplete metamorphosis demands a high expenditure of energy. It is connected with the necessity of large amounts of yolk accumulated in the eggs and is related to a fixed duration of the life cycle. A complete metamorphosis is energetically more economical. It gives better possibilities for variation of the life cycle and the rate of development, which is more advantageous in extreme polar conditions. The only insects with an incomplete metamorphosis which retain a high cenotic significance in the Arctic are the stoneflies (Plecoptera). This is noteworthy because this order has a life history different from the other Hemimetabola. The development of the Plecoptera is very prolonged, with aquatic carnivorous nymphs and adult forms consisting of terrestrial flying insects with limited feeding.

The proportions of taxa in the tundra biota are essentially different from those in the boreal forest belt. This can be observed in the various groups that differ widely in biology and size, including microorganisms and soil algae (Table 16.16). Biotic changes in the high latitudes consist not so much of the reduction of species richness as of the loss or lowering of the cenotic significance of some large taxa, while other large taxa maintain or even increase their importance in the functioning of the ecosystems. Among vascular plants, the genera *Draba*, *Pedicularis*, and *Ranunculus*, in addition to the genus *Saxifraga* already mentioned, all have higher species numbers in tundra communities than in forest stands. This is also true in the Animal Kingdom, for instance, for springtails of the genus *Isotoma*, for craneflies (*Tipula*) (Fig. 16.21) and for sandpipers (*Calidris*).

Every large group of arctic biota has its own peculiarity of macrocomposition. Nevertheless, it is necessary to emphasize once more that the tundra biome is rather heterogeneous. The floristic and faunistic composition of each tundra subzone is peculiar to approximately the same extent as the distinctions between the tundra and the biota of other zones. This is mainly reflected in the changes in the significance of the different taxa (see Tables 16.4, 16.5). The cenotic role of higher groups (families, orders) changes completely northwards from the southern tundra subzone to the polar desert. The main dominants among vascular plants in the southern tundra vegetation are willows and birches, in the typical tundra sedges, *Dryas*, and dwarf-shrubs, and in the arctic tundra grasses and dwarf-shrub willows. Vascular plants lose their dominance in the Eurasian polar desert,

TABLE 16.16

Soil algae: number of species of main orders in Taymyr local floras[1]

Taxon	Tundra subzones			Polar desert (Cape Chelyuskin)
	Southern (Kresty)	Typical (Tareya)	Arctic (Dikson)	
Cyanophyta				
Chroococcales	26	11	6	8
Nostocales	21	11	16	13
Oscillatoriales	48	34	28	19
Chlorophyta				
Chlorococcales	36	34	28	18
Ulotrichales	11	11	7	4
Volvocales	23	15	14	6
Xanthophyta				
Heterococcales	21	14	18	10
Tribonematales	7	6	1	1
Bacillariophyta				
Raphinales	25	12	9	15
Total[2]	238	157	131	100

[1] From Dorogostaiskaya and Sdobnikova (1973), Sdobnikova (1986), and unpublished data given to authors.

[2] Also including Araphinales, Chlorosarcinales, Desmidiales, Discoidales, Entophysalidales, Heterocloniales, Microsporales, Oedogoniales, Pleurocapsales, Stigonematales, Zygnematales.

where mosses and lichens predominate; as shown earlier, there are also important changes in the fauna.

The facts confirm the idea that higher taxa behave as single units when the structure of a biota is changed. Despite the infinite ecological species diversity, one can evaluate the adaptive potential of a group as a whole. In other words, flora and fauna are characterized by a certain organization not only at the species level, but also at a higher taxonomic level – that is, they have a distinct "block" structure. Thus, the main features of tundra biota do not only consist of the progressive lowering of the total taxonomic diversity and richness of the organisms. The spectrum of taxa in the tundra biota is unique.

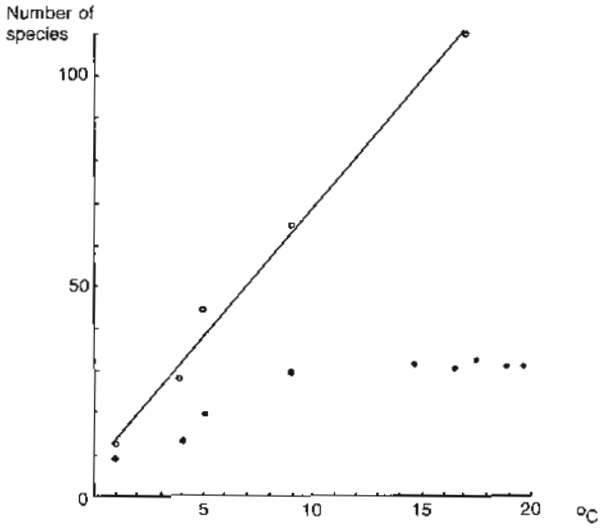


Fig. 16.23. Correlation of the number of species of Collembola with mean July temperature. Open circles represent the number of species in all landscape elements, solid ones in "zonal" plant communities. From Ananjeva et al. (1987).

SPECIES STRUCTURE OF ARCTIC COMMUNITIES

Considering any problems of synecological organization, one must keep in mind the species structure of the community – richness, dominance, diversity, completeness, deficiency, etc. This aspect of community analysis corresponds to the concept of alpha-diversity that comes from classical works by R.W. Whittaker (1965, 1977). All indices of the immanent structure are expressed in its species composition. Therefore, the concept of species structure of communities is widely used in ecology.

The species structure of tundra communities is characterized by many features connected, first of all, by the qualitative impoverishment and reduction of the potential number of species participating in the formation of cenotic groups. The high specificity of variation in the species structure of the communities in the tundra zone is caused by the gradient of the total taxonomic diversity from relatively high in the southern part of the zone to vanishingly low at the northern limit of life. At the same time, the various groups of organisms demonstrate rather diverse relationships in the indices of community species structure owing to their specific biological features and overall taxonomic diversity.

Number of species, species richness

As is well known in all types of communities, the number of species with low abundance significantly exceeds the number of common species.

In the High Arctic latitudes, the relative number of such species becomes lower. Naturally, the environmental capacity, the very possibility of coexistence of many species under severe conditions, is also much lower. In the tundra zone, a higher proportion of all possible species take part in the formation of the biocenosis. In each community or at any site, one can find a relatively large proportion of species that occur in the biome as a whole (Chernov, 1978b, 1985).

In the polar desert where the biota is extremely poor, at any site with all variants of "zonal" plant communities represented, one can find all or almost all species of any taxonomic group in the local flora and fauna. Thus, on Cape Chelyuskin (Taymyr), only 12 species of springtails were recorded, with 9–10 (up to 80%) of them usually being found in every element of nano- or microrelief (Figs. 16.23, 16.24).

In this case, where the species composition is extremely poor, the ecological amplitude and relative species abundance are maximized. To the south, in the arctic tundra subzone, where the local fauna includes 3–4 times as many species, 15–20 springtails have been found in each "zonal" plant community – half of the local Collembola fauna. Further to the south, in the typical tundra subzone the number of springtails in the *Dryas*–sedge–moss communities on "plakor" increases to 30 species,

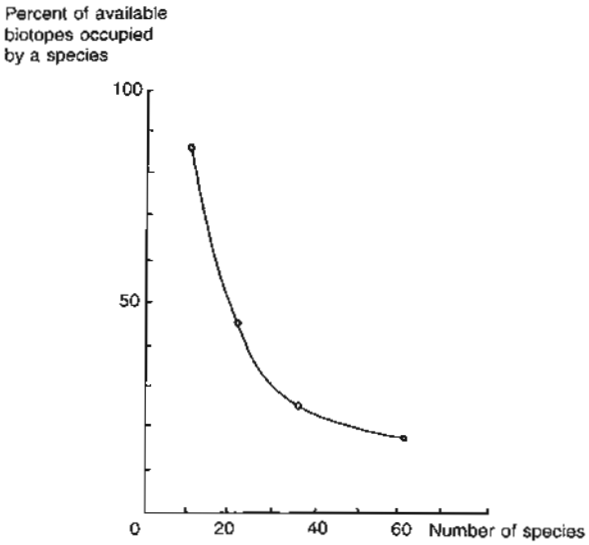


Fig. 16.24. Average percentage of available biotopes occupied by a species of Collembola in relation to the number of species in the local fauna. From Ananjeva (1973), Ananjeva and Chernov (1979), Chernov et al. (1979) and Ananjeva et al. (1987).

which constitute even less than half of the local fauna of this group.

Concurrently, the ecological amplitude of species becomes narrower – that is, the number of biotopes occupied by a species is reduced (Fig. 16.24). In the forest landscapes where the whole Collembola fauna is much greater, their number in the main "zonal" plant communities remains at approximately the same level as in the typical tundra (30–35 species) (Peterson, 1982; Kuznetsova, 1984; Ananjeva et al., 1987). This can be considered as evidence that the number of species that can coexist in the same community is rather low, which in the case of springtails is already reached in the typical tundra subzone. These comparisons are based on approximately the same number of samples (several dozens in each case).

Table 16.17 shows the number of vascular plants in the main Taymyr "zonal" plant communities. There is no reduction northward in the number of species in a plot of a given size along the whole sample-plot gradient. One can even say that the species concentration in a given plot size is less in the typical and southern tundras than in the arctic–tundra subzone, even though the total number of species of vascular plants in the arctic–tundra flora is about half that further south. Thus, species "saturation" of certain parts of the communities already occurs in the arctic tundras. These data can be considered as an indicator of a certain structural stability of "zonal" communities. Despite considerable climatic variations, this feature of their structure does not change.

The data in Table 16.17 also show an increased rate of appearance of new species with increases in the size of the sample plots as one proceeds from the southern to the arctic tundras. For example, to record an average of 30 species, a sample of 10 m^2 is required in the arctic tundra, in the typical tundras over 50 m^2, and in southern tundras more than 160 m^2. The richer the flora, or the higher the number of potential species taking part in the formation of a community, the larger is the minimum area of the community. The poorer the local flora, the higher is the relative and sometimes even absolute species concentration in the communities.

In the case mentioned above, the horizontal structure of vegetation cover is largely responsible for the species distribution within the "zonal" communities. Along with the worsening climate northward, the size of the elements in a nanorelief mosaic decreases while their numbers per unit area increase (Chernov and Matveyeva, 1979). A high

TABLE 16.17

Number of species of flowering plants in the *Dryas*–sedge–moss frost-boil community type on Taymyr in plots of different size (four replicates)

Subzone	Area (m^2)										Local flora
	0.01	0.04	0.16	0.64	2.56	10.24	40.96	163.84	655.36	2221 44	
Southern tundra (Kresty)	4	7	7	9	10	16	26	28	45	45	241
Typical tundra (Tareya)	3	5	9	11	16	23	26	32	38	49	217
Arctic tundra (Dikson)	5	8	16	22	27	33	37	41	42	50	134

heterogeneity of the plant cover is the cause of the increase in species concentration per unit area (Table 16.18).

The character of the species concentration and distribution per unit community area is specific for every community type. It depends on the horizontal structure of plant and soil cover and on cenotic and population interrelationships. The spatial distribution of species or groups of species is reflected in the species/area curves (Fig. 16.25).

The examples given show that species number as a synecological parameter is highly relative. In comparative analyses of the tundra communities, it can only be used with certain care. The number of species in the local flora or fauna, their variety, and consequently their availability to form the communities play a specific role.

Species with wide ecological amplitudes in relation to heat and nutrients have certain advantages in extreme environments. The important feature of a species, enabling it to flourish in the High Arctic latitudes, is high phenetic plasticity – that is, the ability to form different life or growth forms. The presence of such species compensates for taxonomic poverty.

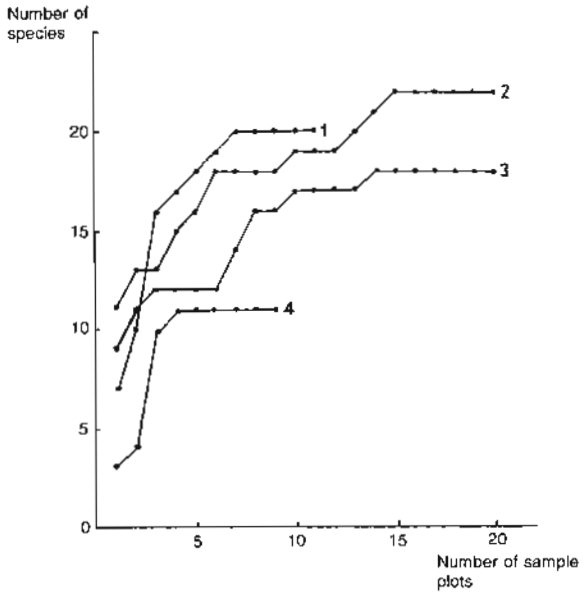


Fig. 16.25. The increase in the number of Collembola species in relation to the number of sample plots in the typical tundra subzone in Taymyr. 1, patches of bare ground being overgrown in a *Dryas*–sedge–moss frost-boil community; 2,3, two sites in *Dryas*–sedge–moss hummocky communities; 4, continuous cover in a *Dryas punctata* heath. From Chernov (1978b).

Species richness and abundance values in communities

In the specific environments of the tundra, species number is generally reduced. At the same time, however, some species which can do well under the conditions receive a certain advantage. The lower the taxonomic diversity, the higher is the population density of the species resistant to the adverse factor. In other words, the taxonomic impoverishment is compensated for by an increase in the population density of the remaining species. The total density may exceed that which is typical for

TABLE 16.18

Number of species of flowering plants (in a 100-m^2 sample plot) in different elements of nanorelief in the *Dryas*–sedge frost-boil community type on Taymyr

Element of nanorelief	Southern tundra subzone	Typical tundra subzone		Arctic tundra subzone	
	(Kresty)	Southern part (Tareya)	Northern part (Rogozinka)	Southern part (Dikson)	Northern part (Maria Pronchishcheva Bay)
Patches	33	41	30	32	27
Rims	35	48	39	23	–
Troughs	19	36	23	28	15
Total	61	57	50	50	34
Number of mosaic units (patch-rim-trough)	17	32	60	90	144
Number of species in the local flora	241	217	205	134	96

more taxonomically diverse communities. In different parts of the tundra zone, a negative correlation between species diversity and abundance is especially pronounced, and in very different taxonomic groups (Chernov, 1978b). This can be shown in some examples of tundra animals.

In the northern part of the tundra zone, small rodents are represented by only two lemming species. Their density, however, especially in years of maximum abundance, is certainly higher than that of the whole complex of small rodents in forests which include many more species. If the density values are calculated not only per unit area, but also by taking into account the environment resources (for instance, plant productivity) then the excess in the total abundance of the tundra rodents is even more significant.

These regularities can be even better observed in soil invertebrates, which include a greater number of species, for instance of Collembola, which are well adapted to the arctic environments. The taxonomic diversity of Collembola decreases significantly from the deciduous forests to the polar deserts (Fig. 16.23). There are about a hundred species in the southern tundra, about 70 in the typical tundra, 30–40 in the arctic tundra, and only about 10–12 in the polar desert. Nevertheless, the total abundance (numbers) increases with the latitude (Chernov, 1975; Peterson, 1982; Ananjeva et al., 1987). In coniferous forests, the total density is about 300 dm^{-2}, with large variations. In the typical tundra subzone, similar or somewhat greater values are recorded, normally about 350 dm^{-2}. In the arctic tundras, 500 dm^{-2} is the usual value for their density, with 700 dm^{-2} as a maximum. In the polar desert, this value is usually 500–700 and may even exceed 1000 dm^{-2}. Thus, in this case the inverse dependence between population density and species richness is obvious.

Similar relationships are observed in another invertebrate group, the beetle mites (Oribatei). Their species number and population density are significantly less in the tundra zone than in the forest belt, where they occupy the leading position among soil microarthropods. Their species number continues to decrease northward within the tundra zone, but their density in the northernmost regions seems to increase. Thus, there are 33 species of Oribatei in the fauna of the typical tundra subzone in the Taymyr, with a density in the main "zonal" communities of about 20 dm^{-2}, while in some warmer "intrazonal" biotopes, this value exceeds 100 dm^{-2}. In the arctic tundra subzone, there are only 9 species, but their density in "zonal" communities is as high as 60–150 dm^{-2}. A reduction in species richness decreases the interspecific competition, but the population density of particular species also depends on general cenotic and abiotic factors. The numbers of Oribatei are in all cases lowest in communities with a thick moss layer (Ananjeva et al., 1973, 1979). In the arctic tundra subzone, the moss layer is disrupted. There are many patches of bare ground, which, in spite of the generally severe climatic conditions, are relatively warm and favorable for Oribatei breeding.

The increase in density can be related to the reduction in species richness not only of that taxon but of all organisms of the ecosystem in question. As mentioned above, larger taxa behave as ecological units. The biotic changes in High Arctic latitudes are not necessarily caused by the reduction in diversity of the whole biota, but by the disappearance or reduction of the significance of some large taxa against the background of relative richness of other taxa.

Most interesting in this connection are the polar desert communities which are particularly poor in all invertebrate species (Chernov et al., 1979). The "core" of soil invertebrate communities is formed mainly by four groups: namely, Nematoda, Enchytraeidae, Collembola, and the larvae of Chironomidae. Other groups (Gamasida, Tardigrada, and the larvae of Mycetophilidae) play a significantly smaller role. The taxonomic composition of the polar desert "zonal" communities is practically limited to these groups. All others, including the larvae of Tipulidae and Trichoceridae, are only distributed locally. The species numbers in all groups are extremely small, many of them being represented by very few or even by a single species. However, along with a significant reduction in species richness, the density of many invertebrates and their biomass in the very thin soil cover is relatively high in the polar deserts. The densities of Enchytraeidae and Collembola and larvae of Chironomidae and Mycetophilidae sometimes exceed those of the same groups in other "zonal" landscapes. Thus, the density of larval Chironomidae in the polar desert may be about 500–1500 m^{-2}, which is much greater than in any other type of terrestrial community. Elsewhere, this group reaches high density values only in water pools as part of the benthos. The density of Enchytraeidae

is at the same level as in the arctic tundras, 10–70 dm^{-2}. Collembola numbers in polar deserts, however, reach about 1000 dm^{-2} and sometimes even 3000 dm^{-2} (Chernov et al., 1977; Bulavintsev and Babenko, 1983) and exceed all values known for other "zonal" landscapes.

As a result of such high population densities, the total zoomass in polar deserts may be relatively high (5–10 g m^{-2} fresh weight) – that is, only a little less than in the typical tundra subzone. This value of course is especially high if one takes into consideration the very thin soil cover.

The arctic tundra communities are not as poor taxonomically as the polar deserts. There are many taxa which are typical of the arctic biota. However, compared with zones further south, their species richness is reduced. For example, in the "zonal" communities of "plakor" in Taymyr arctic tundras, important taxa such as Lumbricidae, Carabidae, Chrysomelidae, Staphylinidae, and Tipulidae are only represented by very few species (Table 16.19). That is why the structure of the cenotic complexes is very simple. Many important biocenotic compartments consist of a single species only. The result of such structural simplification is the relatively high density of each species. Thus, the total mesofauna zoomass in the arctic tundras is often very high – certainly higher than in the "zonal" communities of typical tundra. In arctic tundra, the fresh zoomass is about 20 g m^{-2} (varying from 10 to 50 g m^{-2} in different mosaic elements), whereas in the typical tundra it is 7–10 g m^{-2} in "zonal" communities and 50–100 g m^{-2} in the herb–dwarf-shrub communities on the southern slopes. Thus, the mesofauna zoomass of "plakor" in arctic tundra is similar to that of the optimal "intrazonal" communities of the typical tundra subzone.

The inverse dependency between the density and species richness of a community is therefore rather general. It has been recorded for different organisms (vascular plants, mosses, springtails) which form anthropogenic communities. The springtails have a maximum density in communities where their species composition is very poor — for example, in *Dryas* heaths at the edge of high river banks. There is very little snow in winter in such habitats and they are relatively dry in summer. The species diversity of Collembola in such communities is very low, but the density of each of the few

TABLE 16.19

Invertebrate mesofauna, numbers (dm^{-2}) and live mass (μg fresh weight dm^{-2}), in the elements of polygonal *Salix polaris*–moss communities on northeastern Taymyr[1]

Groups and species	Bare ground		Mossy strips		Lichen cushions		Vascular plant mats	
	No.	Mass	No.	Mass	No.	Mass	No.	Mass
Annelida								
Enchytraeidae	5.0	10	15	32	9.0	21	56.8	85
Lumbricidae								
Eisenia nordenskioldi	0.8	120	0.8	100	0.3	45	3.2	300
Arthropoda: Arachnida								
Araneae								
Erigone psychrophila	0.1	0.6	0.4	2	0.2	1	0.8	5
Insecta: Coleoptera								
Staphylinidae								
Larvae and adults of *Tachinus arcticus*	1.0	4	0.4	0.5	2.0	9	0.8	3
Chrysomelidae								
Larvae and adults of *Chrysolina subsulcata*	0	0	0	0	0.1	3	0.5	16
Insecta: Diptera								
Tipulidae								
Larvae of *Tipula carinifrons*	0.2	40	0.4	60	0.3	35	1.7	153
Larvae of other Diptera	0.1	0.5	0.1	0.6	0.4	2	0.5	3

[1]From Chernov (1978b).

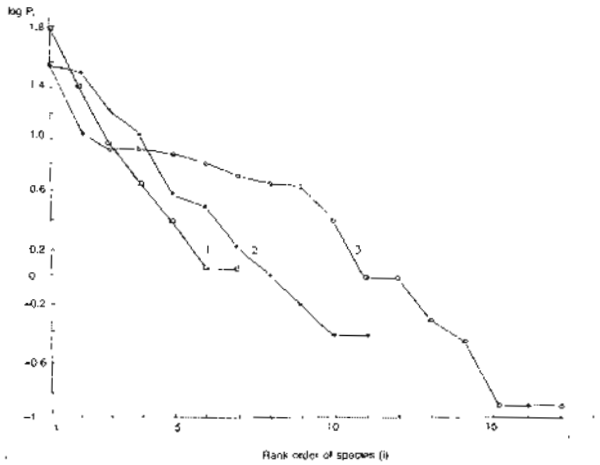


Fig. 16.26. Curves of relative dominance of Collembola in the arctic tundra subzone in Taymyr (Dikson). See footnote next page. 1, patches of bare ground; 2, patches of ground being overgrown; 3, troughs; P_i, relative abundance, % of total; i, species. From Ananjeva et al. (1987)

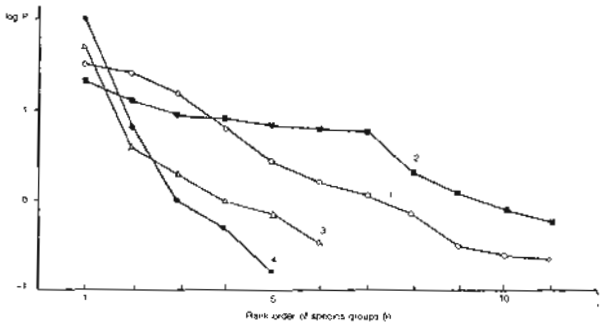


Fig. 16.27. Curves of relative dominance in yeast groupings at different stages of leaf decomposition of *Carex ensifolia* ssp. *arctisibirica* in the northwest Taymyr. See footnote. 1, green leaves; 2, dead dry unbroken leaves; 3, decomposing leaves; 4, humus. From I.Y. Chernov (1985).

Onychiurus species and of *Xenyllodes armatus* reaches 600 dm^{-2}. This is the highest population density of a single species recorded in the typical tundra (Chernov, 1978b). These few species are responsible for a maximum total density of 1500 dm^{-2}.

In general, the maximum density of communities is determined by the high density of very few species. This principle manifests itself in particular in the extreme environments.

Dominance

Predominance of a relatively small number of species is the general principle of organization of the majority of tundra communities. The ratio of the quantitative indices of the dominants to the abundance indices of the community as a whole can serve as a measure of dominance. However, to find a common measure for dominance in diverse types of communities is a difficult task. It is possible that dominance indices in the tundra communities are not higher than those in the forests or in the steppes; however, in the tundra zone the set of dominants is poorer and more stable, and thus more noticeable.

Dominance as a phenomenon is a consequence of deviation of the environment from conditions favorable for a large number of species (as in the tropical rain forest). The more specific and generally more extreme the environment, the more marked is the dominance and the greater the differences between the abundances of species. This is a general rule which is well illustrated by curves of dominance [Collembola in Fig. 16.26; microorganisms (yeasts) in Fig. 16.27].[1] Dominance increases with species impoverishment only to a certain level. In the most severe conditions, there are sometimes no species which are able to increase their abundance markedly, so that their population densities become approximately equal and not high. Some complexes of Collembola in the polar deserts and Oribatei in the arctic tundras are good illustrations of this fact (Tables 16.20, 16.21).

One species, *Folsomia regularis*, may constitute 60% of the total Collembola numbers in polar deserts. The dominance of a single species gives a maximum in total numbers and abundance of this group. In some other communities where half or one-third of the Collembola species have high numbers, there are, however, no obvious domi-

[1] In these curves, the species are placed in decreasing order of relative dominance P_i, defined as $P_i = \frac{100 A_i}{\sum_1^n A_i}$, where A_i is some appropriate measure of abundance, such as a population density, of the i'th species. In Collembola, the most peculiar biotope is bare ground for which the curves of dominance are mostly steep. There are many yeast species with approximately equal abundance on the dry but intact leaves which are the most favorable substrate for this group. Decomposing leaves and, in particular, soil are much more specific substrates, so that the number of yeast species is strongly reduced while their abundances differ markedly.

TABLE 16.20

Numbers (dm^{-2}) of Collembola in communities in the polar desert on Cape Chelyuskin[1]

Species	Lichen–moss polygonal fell-field with 5% cover			Moss–lichen cushion community with 20% cover			Lichen–moss polygonal community with 40% cover		
	Stony ground	Lichen crusts	Mossy cushions	Bare ground	Mossy lichen strips	Moss cushions	Bare ground	Moss strips	Wide moss strips
Agrenia bidenticulata	26	18	13	44	23	24	32	21	20
Ceratophysella longispina	2	5	12	0	2	14	0	0	0
C. nivalis	2	4	51	0	20	68	2	34	1
Folsomia regularis	23	76	1186	10	1124	1843	330	664	290
F. taimyrica	1	28	298	12	366	760	106	238	124
Hypogastrura tullbergi	8	18	90	30	240	349	298	96	79
Hypogastrura sp.	5	6	52	16	41	61	48	20	17
Isotoma sp.	2	6	1	12	2	2	1	25	6
Onychiurus sp.	0	0	0	0	0	0	10	37	37
Vertagopus brevicaudus	25	13	172	63	124	102	87	124	21
Total (including unidentified and young)	94	174	1875	190	1942	3663	914	1262	595

[1] From Chernov et al. (1979).

nants. On bare ground or under thin lichen crusts, the number of springtails is not reduced, although the population densities are low and none of the species is abundant.

The number of Oribatei species in the arctic tundras is approximately the same as that of Collembola in the polar deserts (Tables 16.20, 16.21). However, if Collembola literally fill every biotope in the polar deserts, no species of Oribatei has an abundance comparable to the population density of this group in other environments. In the forest belt, the density and species richness of beetle mites are higher than those of springtails. In the arctic tundras, no species of Oribatei can be

TABLE 16.21

Numbers (dm^{-2}) of Oribatei in communities in the Taymyr arctic-tundra subzone[1]

Species	*Salix polaris*–moss polygonal community				*Dryas punctata* fell-field community				Grass–forb meadow
	Bare ground	Lichen cushions	Outside of moss strips	Center of moss strips	Bare ground	Outside of *Dryas* mat	Center of *Dryas* mat	*Novosie-versia glacialis* rosette	
Diapterobates notatus	0	1	0	18	1	0	0	40	0
D. variabilis	3	30	6	5	19	39	36	48	0
Fuscozetes fuscipes	0	0	0	0	0	0	0	0	1
Hermannia gigantea	0	0	0	1	0	106	18	4	0
Liochthonius evansi	0	0	0	1	0	0	0	0	0
L. sellnicki	0	5	9	9	1	36	10	1	0
Melanozetes orientalis	1	82	51	21	45	0	12	6	1
Trichoribates trimaculatus	0	0	0	0	0	0	0	0	23
Trypochthonius tectorum	0	22	2	2	0	0	0	2	2
Total	1	440	68	57	66	181	76	101	26

[1] From Ananjeva et al. (1987).

considered dominant. A general restriction of this group by abiotic factors prevents the increase in their abundance in spite of the availability of empty ecological niches.

Because of the marked species impoverishment in the tundra communities, the principle of dominance can acquire somewhat exaggerated forms. It is typical that the majority of species are abundant, while no species are rare or infrequent. In the High Arctic landscapes, the number of species is hardly enough to fill the main ecological niches. Some large and cenotically important taxa are represented there by a few species only. Each of them is important for the function of the cenosis. The main dominating dwarf-shrub in arctic tundras, *Salix polaris*, is the only representative of willows present. In the "zonal" *Salix polaris*–mossy polygonal communities, the most significant phyllophagous beetles, the Chrysomelidae, are represented mainly by *Chrysolina subsulcata* and more rarely by *C. septentrionalis*, the carnivorous carabids by *Pterostichus brevicornis*, and carnivorous staphylinid beetles by *Tachinus arcticus*; spiders are mainly represented by *Erigone psychrophila* and to a lesser extent by *Collinsia spetsbergensis*, the earthworms by *Eisenia nordenskioldi*, the Tipulidae by *Tipula carinifrons*, and so forth. The study of this aspect of arctic biocenoses can give much support to the theory of ecological niches.

The example of the Collembola complex in polar deserts (see Table 16.20) also demonstrates another important peculiarity of the organization of tundra communities. In nearly all the stands involved, the same species, *Folsomia regularis*, shows the highest population density. The dominance of the same species in different communities and cenotic chains is a characteristic feature of the tundra biocenoses. High ecological plasticity, changeability of morphology and size, developmental speed, trophic type, etc. are typical of such species. This phenomenon is referred to as superdominance, and species as superdominants (Chernov, 1985).

This feature of tundra biocenoses was first noticed when trophic relations were studied (Osmolovskaya, 1948; Chernov, 1967). Thus, for example, lemmings are the central links in trophic chains for the overwhelming majority of tundra carnivores, both mammals and birds. The populations of arctic fox and birds of prey depend completely on the state of the lemming population. *Lemmus sibiricus* and *Dicrostonyx torquatus* are typical superdominants. They inhabit a wide spectrum of ecological environments, they constitute a substantial proportion of the aboveground zoomass, and they strongly influence the dynamics of tundra vegetation, which mean they can appropriately be regarded as real "edificators".

The earthworm *Eisenia nordenskioldi* is also a typical superdominant of tundra cenoses. It occurs in almost all tundra landscapes. *Tipula carinifrons* can also be called a superdominant. Its larvae, together with *E. nordenskioldi*, constitute the bulk of zoomass in the majority of communities of arctic tundras (Table 16.19). This cranefly species stands in the center of very diverse cenotic relations and plays a significant role in decomposition processes and in soil formation (Lantsov and Chernov, 1987).

There are also superdominants among tundra plants. One of the most striking examples is given by two closely related *Dryas* species: *D. octopetala* in Europe and *D. punctata* in Asia. They are the main "builders" of the "zonal" tundra phytocenoses from the southern to the arctic tundras and of diverse "intrazonal" herb–dwarf-shrub communities. They form monodominant stands on sands and stony snowless slopes. Two closely related birch species, *Betula nana* and *B. exilis*, play the most significant role in the vegetation cover of the southern tundra from the Kola peninsula to Chukotka. *Carex ensifolia* ssp. *arctisibirica* is the main dominant in the Siberian "zonal" tundra communities from the southern to the arctic tundra subzones, while *Salix polaris* is the superdominant in the diverse communities of the arctic tundra subzone of northern Eurasia. The moss layer of the majority of tundra communities is formed by *Hylocomium alaskanum*.

Superdominance even manifests itself in the world of microorganisms. A typical yeast superdominant is *Cryptococcus laurentii*, which constitutes the major part of yeast populations in diverse Taymyr tundras (I. Chernov, 1985).

Generally, superdominance is a result of the lack of species which are able to occupy diverse ecological niches. In tundra ecosystems, the ecological niches are filled not only at the expense of species diversity, but also, to a great extent, at the expense of plasticity of the most active species. This is especially clear in the arctic tundra subzone where the same set of species form very diverse combinations in different biotopes (Matveyeva and Chernov, 1977). There are many species of vascular

plants common to such different communities as *Salix polaris*–moss polygonal tundras on "plakor" on the one hand and herb meadows on the south-facing slopes on the other.

Because of the qualitative impoverishment of the biota as a result of adverse environments at high latitudes, possible ecological niches are occupied by a very small number of species, which leads to a decrease in the potential community diversity. There are many representatives of large cenotically important taxa which in high latitudes have high ecological plasticity and play a significant role in various communities. Ecological niches have "widened" – a typical consequence of qualitative impoverishment and reduction in competition (Chernov, 1982; Pianka, 1983). All of this serves as the main mechanism of community formation in extreme environments.

Distribution of species abundance

Besides identifying dominants, information on the correlation of abundance values for all species within a community is also very important. The simplest index is the ratio of total numbers (abundance) to the number of species. The curves of dominance/diversity and the Raunkiaer curve based on frequency (or on biomass, cover, or density) also give a good picture of community structure. Indices of information diversity are widely used; among them the most common is the Shannon index (Figs 16.30, 16.31) given below:

$$\overline{H} = -\sum_i P_i \ln P_i$$

where P_i is the relative abundance of species. The ratio of the diversity index to the natural logarithm of the number of species is an index of evenness, which also reflects the community species diversity. Maximum values of diversity index are usually observed when there are many species with equal abundance. It decreases with both the reduction in number of species and the increase in the abundance of very few species.

All these indices are widely used in the analysis of different types of communities all over the world. Comparative analyses of species relationships in tundra synecology are, however, still rare. At present, the data known allow one to conclude that there are also common regularities of species differentiation in tundra communities.

One of the widely known regularities described by Raunkiaer's curve is the following. When the number of species decreases because of particular environmental conditions, the number of species with low frequency also decreases, whereas the proportion of the most frequent species becomes greater. This rule is supported by the data shown in Figure 16.28. The species distribution in *Dryas punctata–Carex ensifolia* ssp. *arctisibirica*–moss frost-boil tundra in the northern part of the typical tundra subzone in Taymyr is described by a classical Raunkiaer curve with the highest number of species of low frequency (left). This community, widely distributed on "plakor", occupies the most mesic habitats. The second curve in Figure 16.28 describes the species distribution in the *Carex stans*–moss mire, which is wet with poor and cold soil. The absolute number of the most frequent and abundant species (class V) is approximately the same in both stands (25 and 23, respectively).

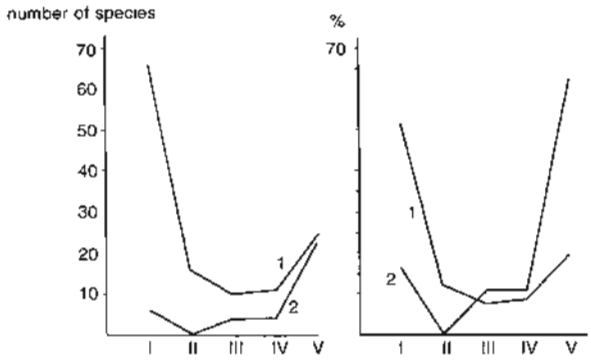


Fig. 16.28. Raunkiaer curves. 1, in a *Dryas*–sedge–moss frost-boil community; 2, in a *Carex stans*–moss mire: A, absolute number of species; B, % of species.

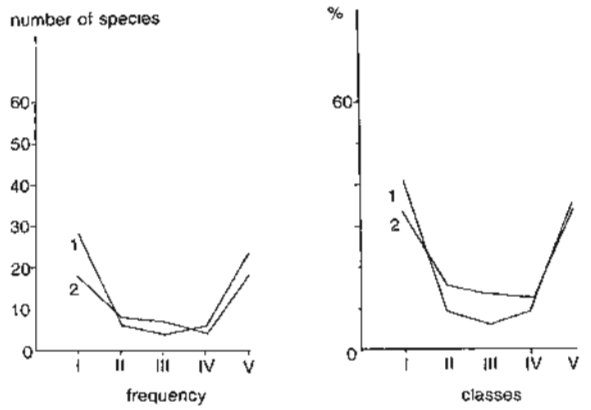


Fig. 16.29. Raunkiaer curves. 1, in a herb meadow on a southern slope; 2, in a *Salix reptans–Carex stans*–moss stand: A, absolute number of species; B, % of species.

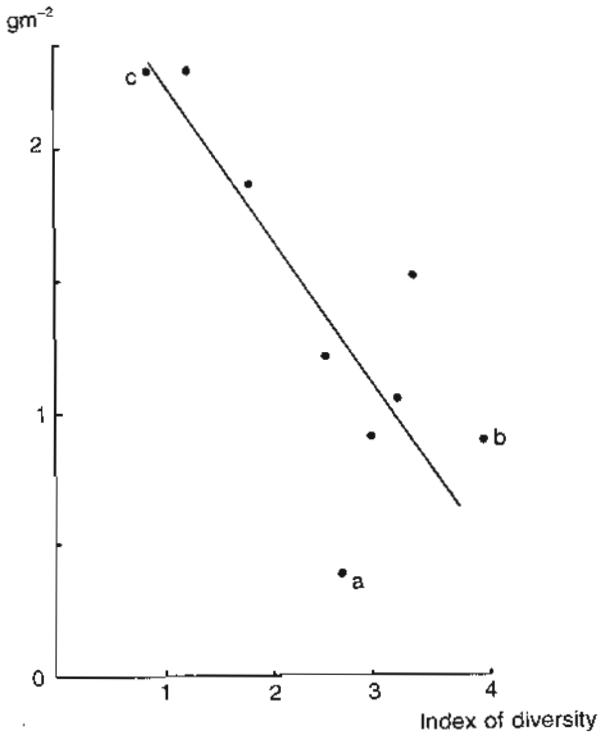


Fig. 16.30. Correlation of a diversity index for Collembola complexes and their total mass in the typical tundra subzone in Taymyr. Each point represents a different type of community. a, patches of bare ground; b, patches of ground being overgrown; c, herb meadow on a southern slope. From Chernov (1978b).

The percentage of species in this class, however, is quite different in the two stands (19.6% and 62.2%, respectively), because of very different total numbers of species (128 and 37). Two other curves (Fig. 16.29) based on data from a herb meadow on a southern slope and from a *Salix reptans–Carex stans*–moss stand in a moist depression also confirm the rule.

There are certain correlations between the distribution of species abundance (information diversity, evenness) and total abundance. The latter is best expressed by biomass values (Giljarov, 1969; Chernov, 1975). A negative correlation has often been found between diversity and biomass. This can be demonstrated in Collembola (Fig. 16.30). The highest diversity indices are obtained for the complexes of springtails occurring on overgrowing patches of bare ground in *Dryas punctata–Carex ensifolia* ssp. *arctisibirica*–moss frost-boil communities with a very fragmentary plant cover, which allows Collembola of very diverse life forms to become established. There are many small forms inhabiting bare ground, so the zoomass is not large. The absence of obvious dominants is not associated with an increase in total abundance and zoomass. The lowest diversity indices are characteristic of meadows on southern slopes where the total number of Collembola is reduced and a few *Onychiurus* species have a high abundance and zoomass. The low diversity index in this case reflects the general instability of this type of community formed in environments not in accordance with the general climatic factors. However, on the patches of bare ground where the mass of springtails is minimal, the index of diversity is also not very high. It is quite possible that the correlation between total biomass and diversity is subject to an optimum rule: minimum diversity indices correspond to both very high and very low biomass values.

There are analogous changes in diversity indices calculated for Collembola and for all soil invertebrates at a family level. In Figure 16.31, communities A–E represent a conditional successional sequence. In such a succession, the highest diversities are characteristic of stages preceding the climax.

Taxa of different size demonstrate very diverse correlations between the indices of diversity. For instance, some microorganisms (yeasts) (Fig. 16.32) have correlations differing from those shown earlier for macroorganisms.

The correlation between the diversity index and total numbers (abundance) depends significantly on the level of species "saturation". When there

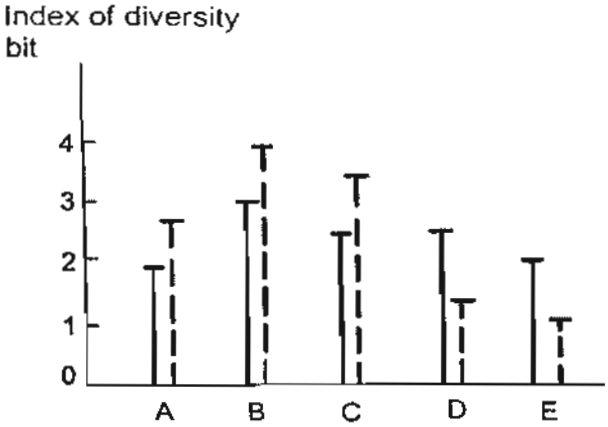


Fig. 16.31. Diversity index of the invertebrate mesofauna as a whole (solid line) and of certain Collembola complexes (broken line) in the typical tundra subzone in Taymyr. A, patches of bare ground; B, patches of ground being overgrown; C, *Dryas*-sedge–moss hummock community; D, herb–*Dryas* community; E, herb–grass meadow on southern slope. After Chernov (1978b).

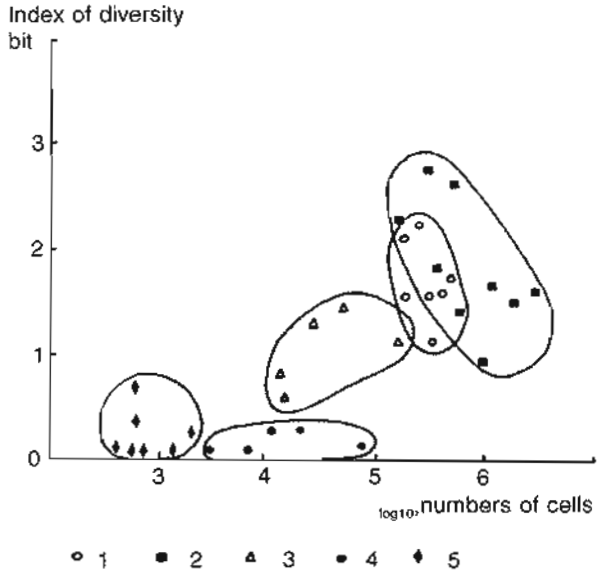


Fig. 16.32. Correlation of a diversity index and $\log_{10}$ of number of yeast cells per gram soil in northwestern Taymyr. 1, green leaves; 2, dead dry unbroken leaves; 3, decomposing leaves; 4, humus; 5, soil. From I. Chernov (1985).

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 differentiated 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 the vegetation cover, but they are followed by the distribution of animals and microorganisms (Chernov, 1978b; Parinkina, 1979c; I. Chernov, 1985) as

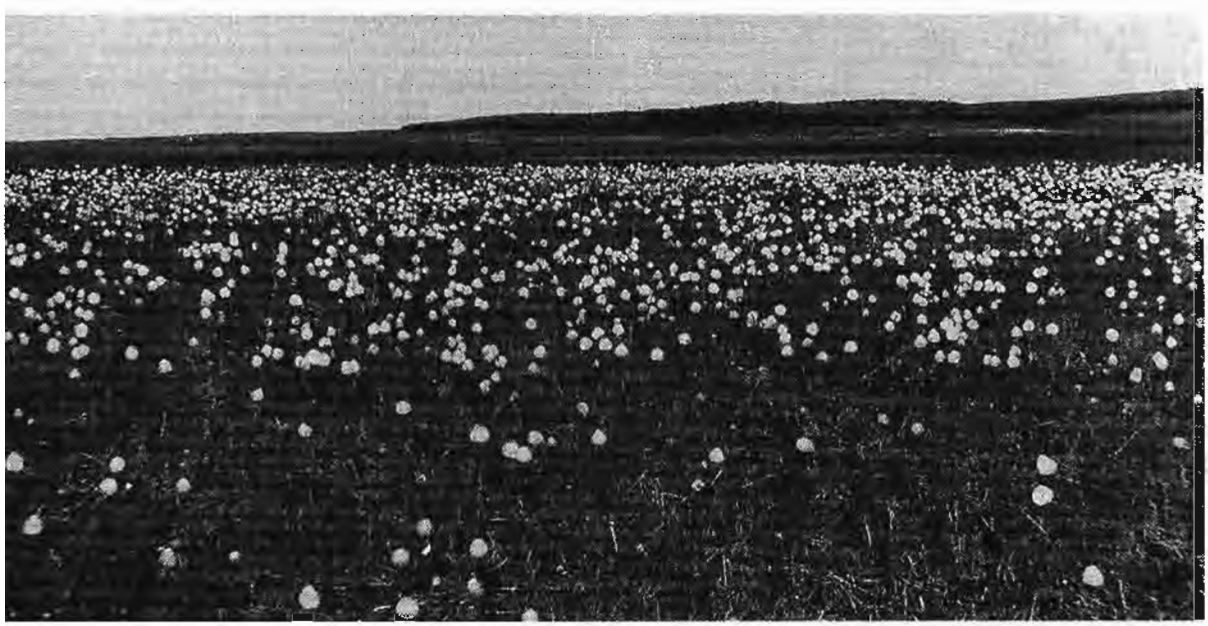


Fig. 16.33. *Eriophorum scheuchzeri* stand with homogeneous vegetation pattern in a river shallow, Kresty, Taymyr.

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 stans*, *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 *Drepanocladus exannulatus*, or combinations of vascular plants and mosses (*Carex chordorrhiza*, *C. rariflora*, *C. stans*, *Cinclidium arcticum*, *C. latifolium*, *Drepanocladus intermedius*, *D. revolvens*, and *Meesia triquetra*) 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*,

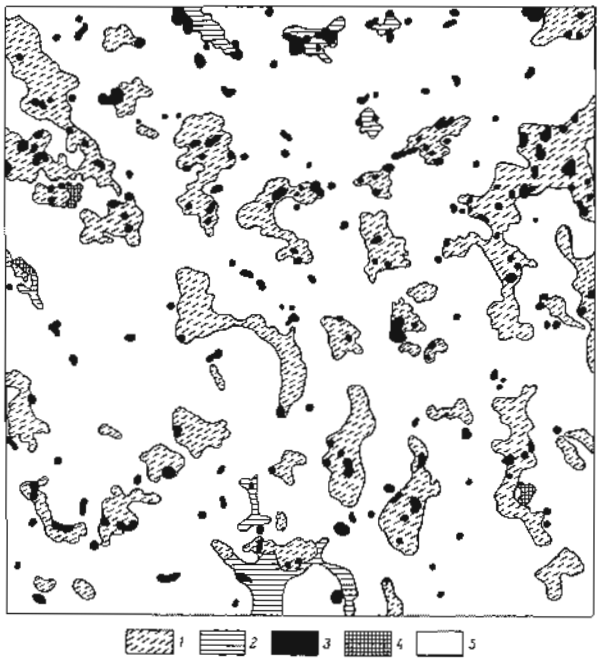


Fig. 16.34. Sporadically spotted type of horizontal structure in a *Dryas punctata* heath on a fell-field in Maria Pronchishcheva Bay, Taymyr. 1, *Dryas punctata*; 2, *Salix polaris*; 3, *Novosieversia glacialis*; 4, moss turf of *Dicranum elongatum* and *Polytrichum strictum*; 5, fell-fields with crustose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

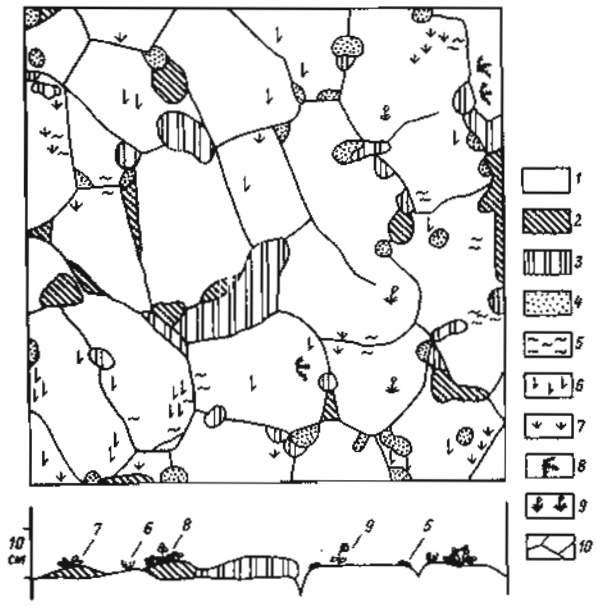


Fig. 16.35. Sporadically spotted type of horizontal structure and vertical profile in a moss–lichen polar desert at Cape Chelyuskin, Taymyr. 1, bare ground; 2, *Orthothecium chryseum*; 3, *Bryum tortifolium*; 4, *Stereocaulon rivulorum*; 5, *Thamnolia subuliformis*; 6, *Phippsia algida*, 7, *Cerastium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

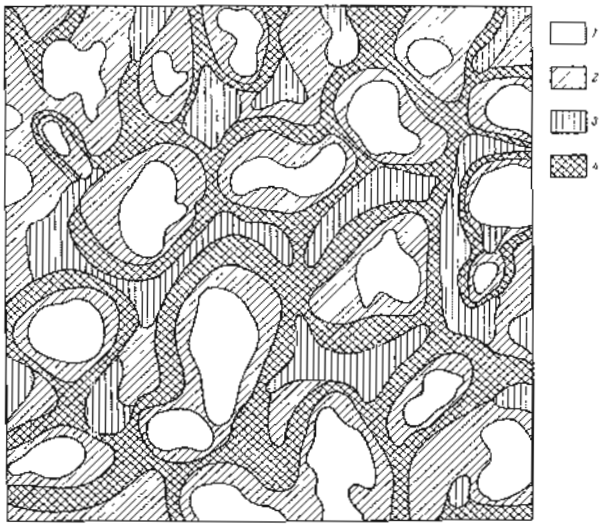


Fig. 16.36. Regular cyclic type of horizontal structure (first variant on a flat surface) in a frost-boil community at Kresty, Taymyr. 1, patches of bare ground in different successional stages; 2, *Hylocomium alaskanum* + *Aulacomnium turgidum* + *Carex ensifolia* ssp. *arctisibirica* + *Dryas punctata*;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

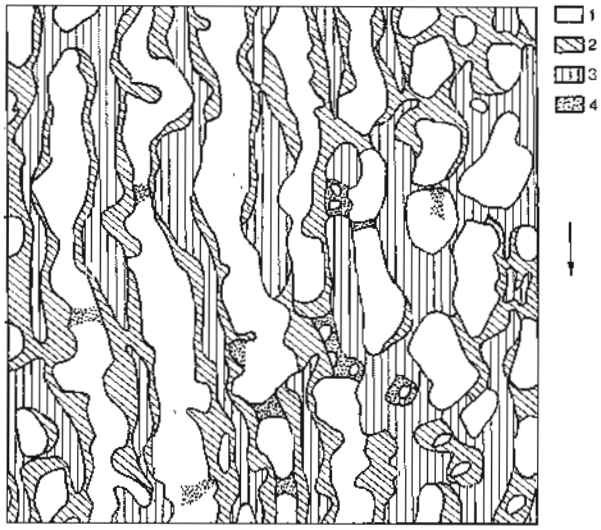


Fig. 16.37. Second variant of a regular cyclic structural type on a slope in the arctic tundra subzone in the mouth of the Uboinaya River, Taymyr. 1, bare ground with solitary vascular plants; 2, border of *Salix arctica* + herbs on the polygon surface; 3, *Hylocomium alaskanum* + *Salix arctica* in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

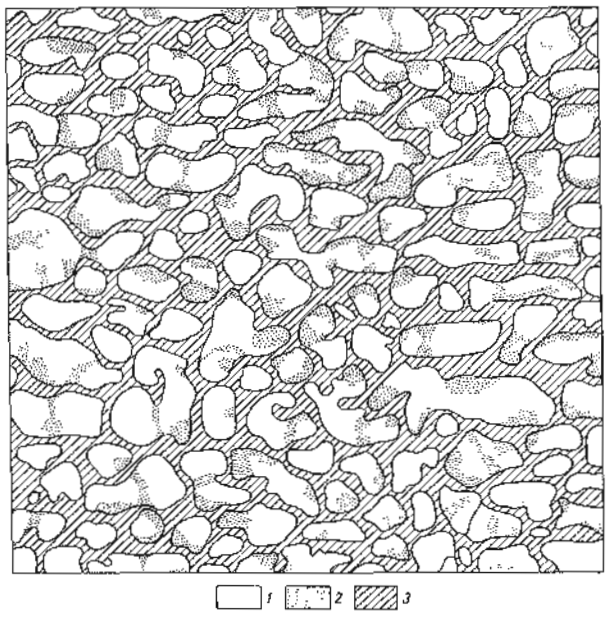


Fig. 16.38. Regular cyclic type of horizontal structure (third, two-element variant) in the arctic tundra subzone in Maria Pronchishcheva Bay, Taymyr. 1, bare ground; 2, solitary vascular plants and crustose lichens; 3, *Hylocomium alaskanum* + *Salix polaris*. Sample plot 10 × 10 m.

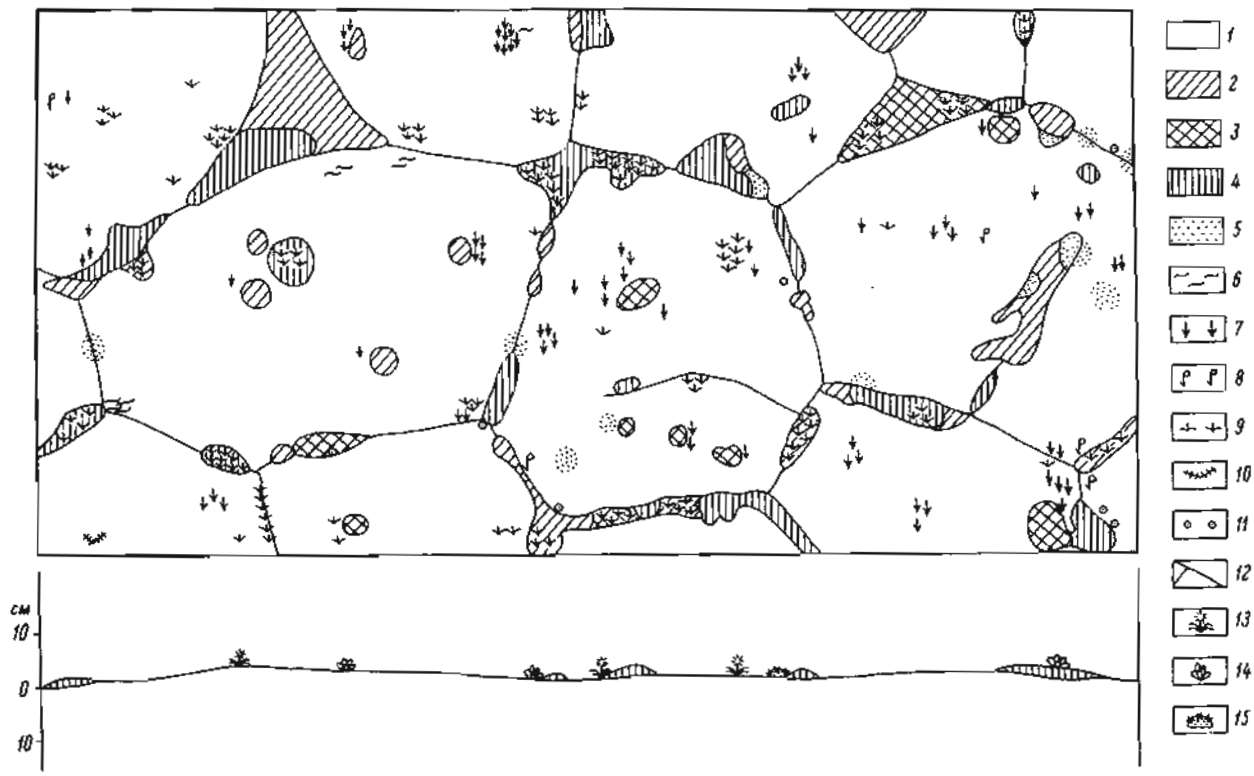


Fig. 16.39. The initial stage of the two-element variant of the regular cyclic structural type in the polar desert at Cape Chelyuskin, Taymyr. 1, bare ground with stones; 2, *Aulacomnium turgidum*; 3, *Bryum tortifolium*; 4, *Orthothecium chryseum*; 5, *Psoroma hypnorum*; 6, *Thamnolia subuliformis*;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

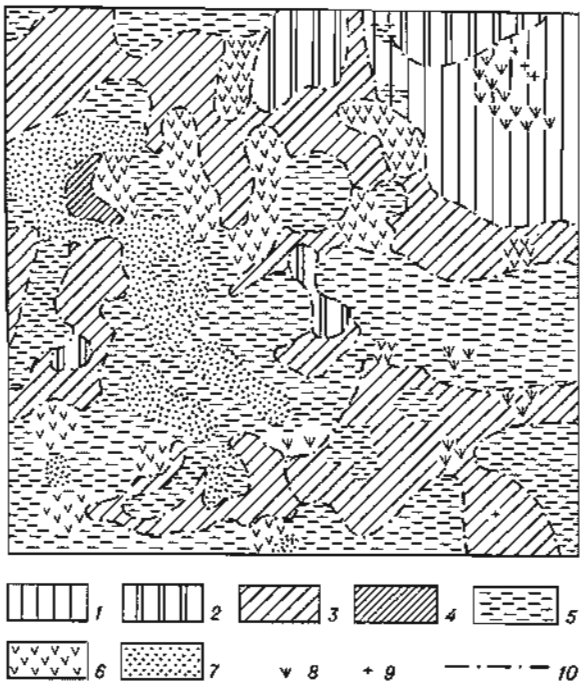


Fig. 16.40. Irregular mosaics in the trough and on the rim in a frost-boil *Dryas*–sedge–moss community at Tareya, Taymyr. 1, *Tomenthypnum nitens*; 2, *Aulacomnium turgidum*; 3, *Hylocomium alaskanum*, 4, *Racomitrium lanuginosum*; 5, *Dryas punctata*; 6, *Carex ensifolia* ssp. *arctisibirica*; 7, foliose lichens (*Nephroma, Peltigera*); 8, *Salix polaris*; 9, *Polygonum (Bistorta) viviparum*; 10, boundaries between plant aggregations. Sample plot 50 × 50 cm.

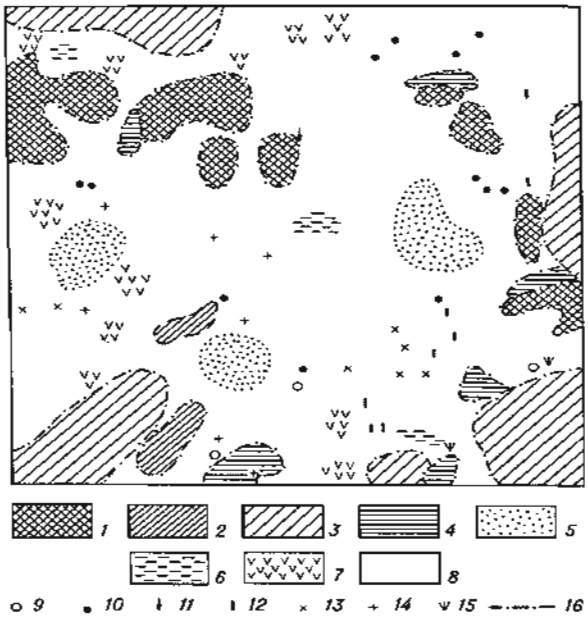


Fig. 16.41. Sporadically "spotted" structure in a frost-boil *Dryas*–sedge–moss community at Tareya, Taymyr. 1, *Dicranum spadiceum*; 2, *Hypnum bambergeri*; 3, *Hylocomium alaskanum*; 4, *Ditrichum flexicaule*; 5, crustose lichens *Tonnia lobulata*, *Baeomyces carneus*; 6, *Dryas punctata*, 7, *Carex ensifolia* ssp. *arctisibirica*; 8, *Festuca brachyphylla*; 9, *Juncus higlumis*; 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 × 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-

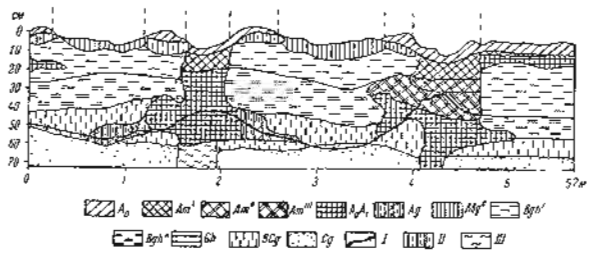


Fig. 16.42. Structure of a soil profile in a frost-boil *Dryas*–sedge–moss community in the typical tundra subzone at Tareya, Taymyr. Letter designations are soil horizons. I, permafrost level in August; II, humus streaks; III, ice wedge. From Ignatenko (1971).

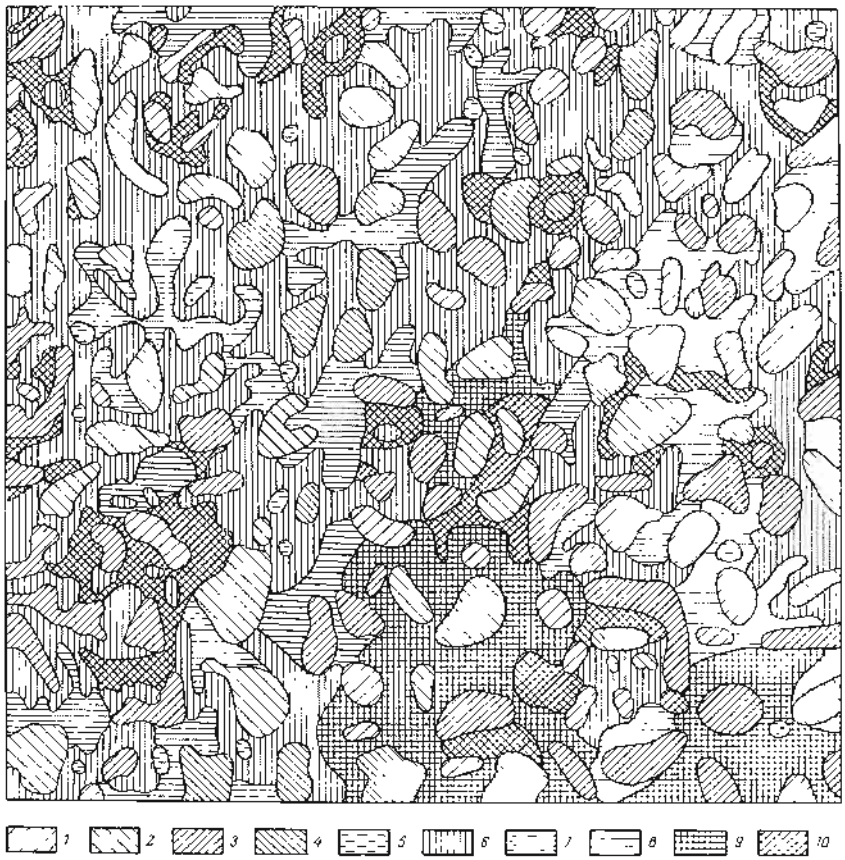


Fig. 16.43. Irregular mosaic structural type in a *Dicranum elongatum–Betula nana–Carex ensifolia* ssp. *arctisibirica* hummocky community in the southern tundra subzone at Kresty, Taymyr. Vegetation on hummocks (1–5): 1, *Ptilidium ciliare* + *Dicranum* spp. + *Aulacomnium turgidum* + *Vaccinium vitis-idaea* ssp. *minus* + *Cassiope tetragona* + *Dryas punctata*; 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*; 7, *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

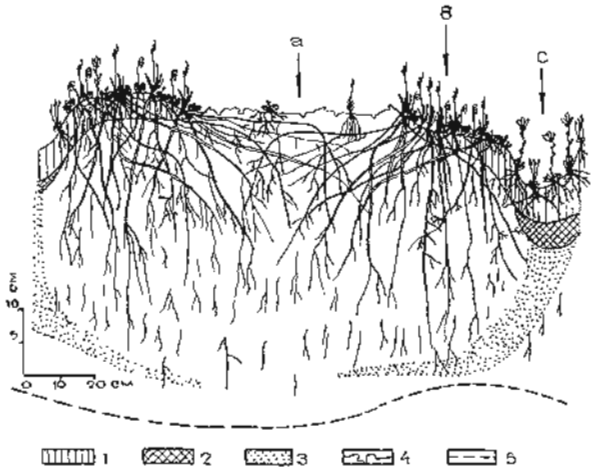


Fig. 16.44. Vertical section in a frost-boil *Dryas*–sedge–moss community in the arctic tundra subzone at Dikson, Taymyr. a, patch of bare ground; b, rim; c, trough; 1, *Hylocomium alaskanum*; 2, dead part of moss turf; 3, peat; 4, surface of bare ground; 5, level of permafrost.

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 3×3 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 5×5 m can be recommended for practical purposes. For homogeneous communities and for those with a sporadically spotted structure, 3×3 m or 2×2 m will be sufficient. These sizes are less than those commonly used for meadow and forest relevés.

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

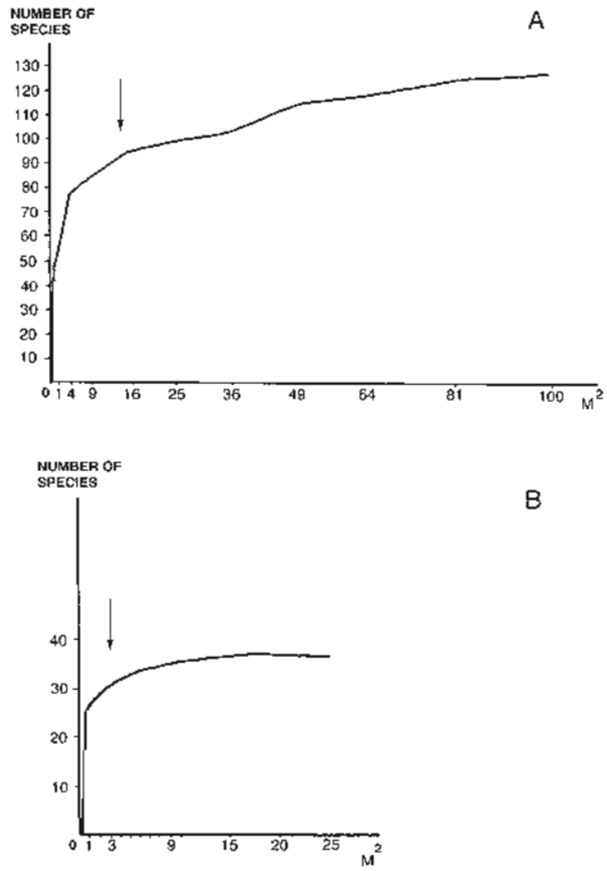


Fig. 16.45. Species number/area correlation in (A) a frost-boil *Dryas*–sedge–moss community with regular cyclic structure and in (B) a *Carex stans*–moss mire with homogeneous structure in the typical tundra subzone in the mouth of Rogozinka River, Taymyr. Arrows show the position on the curves where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

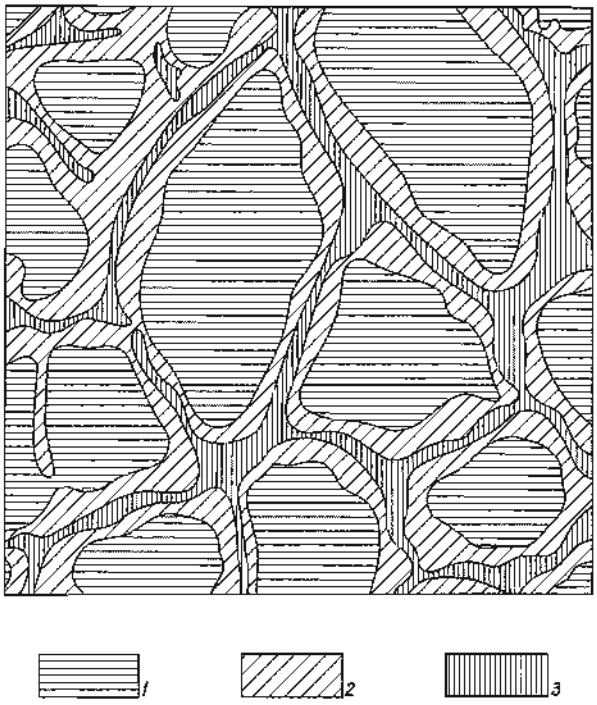


Fig. 16.46. Regular structural type of the vegetation cover in a polygonal mire at Tareya, Taymyr. 1, Saturated center of polygon with homogeneous plant cover; 2, rim with irregular mosaic structure; 3, saturated trough with homogeneous cover. Sample plot 60 × 60 m

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 × 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.

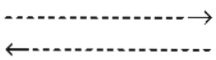
DYNAMIC PROCESSES IN ARCTIC COMMUNITIES

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.

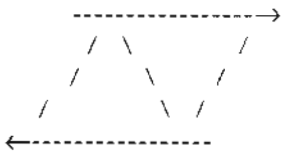
It is, however, problematic to apply the notion of climax to the "zonal" tundra communities. At the terminal stages of development of the living plant cover in High Arctic latitudes, there is no state of stable equilibrium. Changes in the environment resulting from the development of the living cover 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



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



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

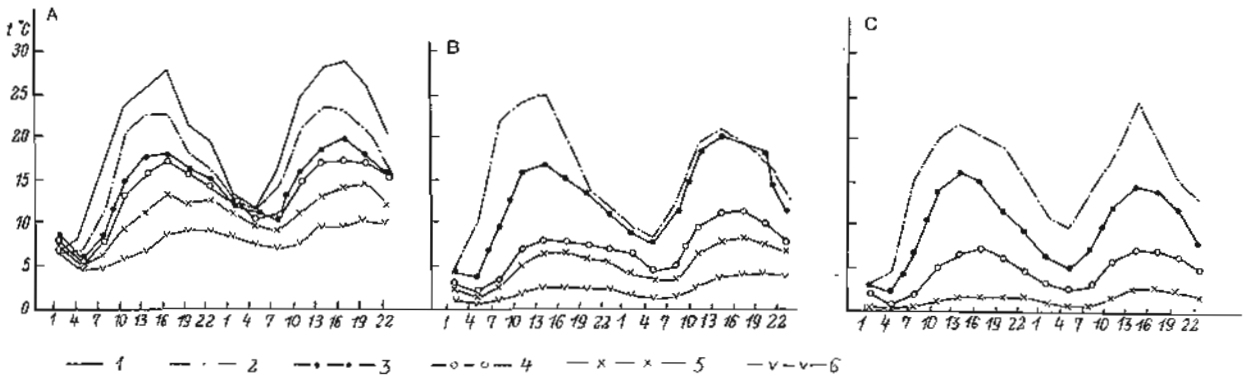


Fig. 16.48. Daily course of soil temperature in different elements of nanorelief in a frost-boil *Betula nana*–sedge–moss community in the southern tundra subzone at Kresty, Taymyr, June 1976. A, patch of bare ground; B, rim; C, trough; 1, air; 2, soil or moss surface; 3, depth 2 cm; 4, depth 5 cm; 5,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

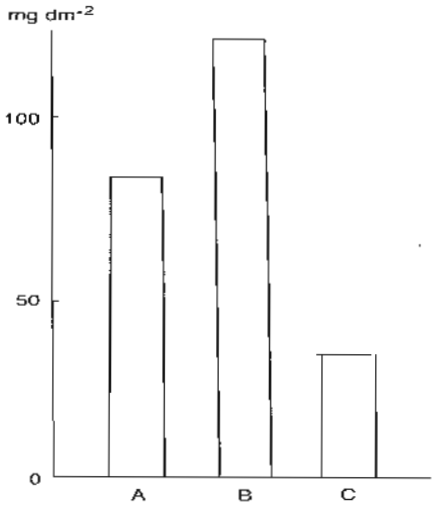


Fig. 16.49. Invertebrate mass (mg, fresh weight) under moss cushions in different polar desert communities with various density of plant cover at Cape Chelyuskin, Taymyr. A, 5% cover; B, 20% cover; C, 60% cover. From Chernov et al. (1979).

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.

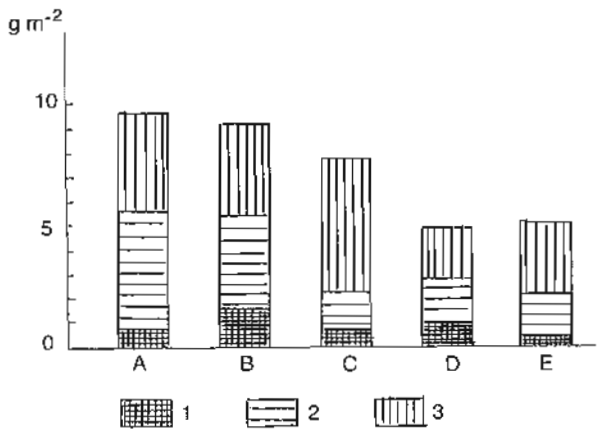


Fig. 16.50. Mass (g, fresh weight) of worms of different groups in elements of frost-boil communities with various density of plant cover in the typical tundra subzone at Tareya, Taymyr. A, patches of ground with crust of crustose lichens; B, patches being overgrown with small cushions of mosses and 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).

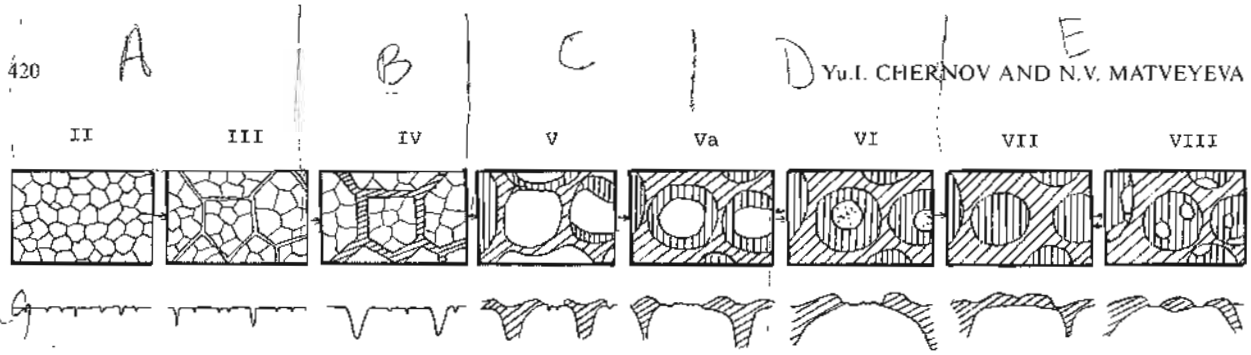


Fig. 16.51. Succession in the formation of "zonal" tundra communities in Arctic. For explanations, see text.

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 extreme conditions 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

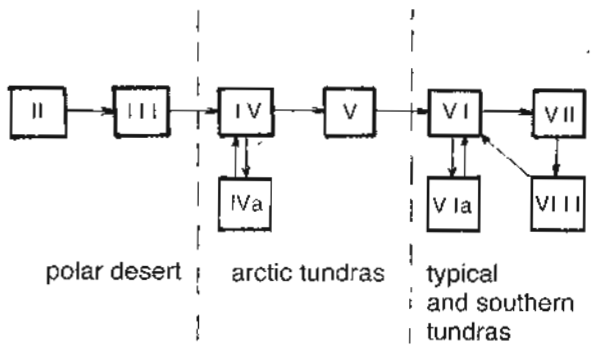


Fig. 16.52. Provisional scheme of successive stages in the formation of "zonal" tundra communities and their representations in different subzones. For explanations, see text.

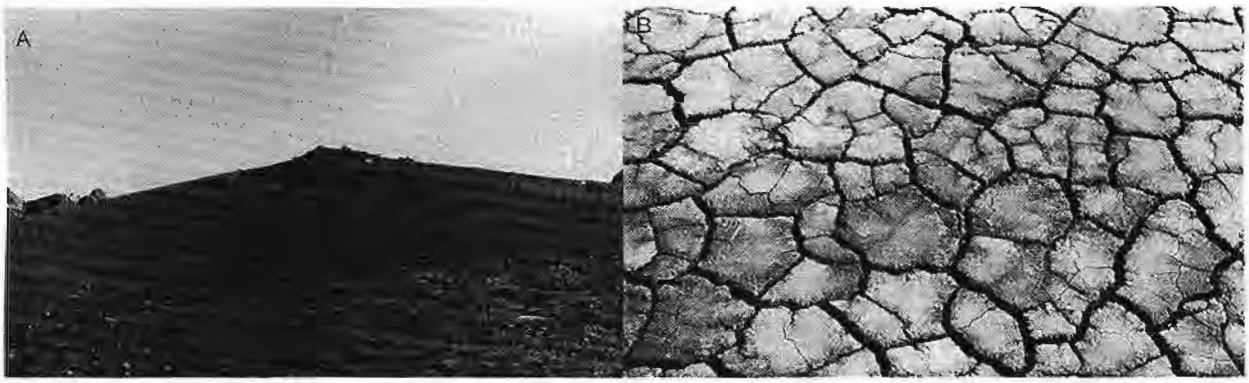


Fig. 16.53. Primary substrate as a result of (A) weathering (Dikson) and (B) water erosion (Rogozinka River, Taymyr).

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.

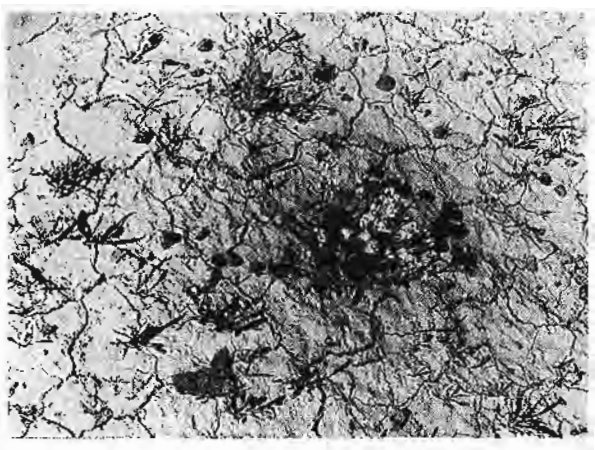


Fig. 16.54. Cracked surface of a solifluction slope with solitary vascular plants (the cracks become closed after rain) by the Rogozinka River, Taymyr.

The second stage (II 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 *Carex 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 julacea*) 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 terminal 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 tornoënsis, 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-*

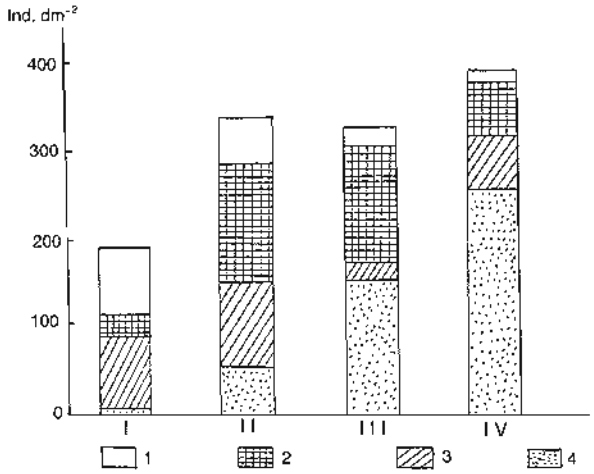


Fig. 16.60. Numbers of different life forms of Collembola in elements of nanorelief in a frost-boil tundra at Tareya, Taymyr, June 1968 (on the basis of 15–30 sample plots). I, patch of bare ground with crust of crustose lichens; II, patch being overgrown with small cushions of mosses and vascular plants; 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 (*Salix pulchra*, *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.

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

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 hyparctica*), grasses (*Deschampsia glauca*, *Festuca cryophila*, *Koeleria asiatica*, *Poa alpigena*, *P. arctica*), 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.

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 7×10 to 20×30 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 rims are elevated by 0.5 m and relatively dry. There is water in the troughs (along the cracks) separating the polygons. Unlike the central parts of the polygons where it is stagnant, water circulates in troughs. Overgrowth of polygonal mires often proceeds simultaneously both in the center of the polygon and around its periphery. At the initial stages, there are no differences in succession between the various elements of the polygonal surface. The first to settle are the hygrophilous grasses (*Arctophila fulva*, *Dupontia fisheri*), sedges (*Carex stans*), and cotton grass (*Eriophorum angustifolium*) which form dense homogeneous stands. The lower layer is made up of herbs (*Caltha arctica*, *Cardamine pratensis*, *Comarum palustre*) and a moss cover of hygrophilous mosses (*Calliergon*, *Cinclidium*, *Mnium*).

As the mosses grow, peat is accumulated in the lower part of the turf. Therefore, the concave surface of the central part becomes gradually flattened and less moist. In the graminoid layer, *Carex stans* is dominant in combination with *Carex chordorriza*, *C. rariflora*, and *C. rotundata*. The moss turf, 5–10 cm thick, is made up of *Calliergon sarmentosum*, *Drepanocladus lapponicus*, *D. latifolius*, *D. revolvens*, *D. vernicosus*, and *Meezia triquetra*, which are later replaced by *Aulacomnium turgidum* and *Tomenthypnum nitens*. Later, dwarf-shrubs like *Cassiope tetragona*, *Dryas punctata*, and *Vaccinium vitis-idaea* also appear, as well as the shrubs *Betula nana*, *Salix pulchra*, and *S. reptans*, at first solitary, and then in masses.

The stage containing shrubs and dwarf-shrubs is already typical for the flat-concave surface. The rims escape first from the state of permanent saturation, and the hygrophilous species of mosses found there are replaced by common tundra mosses such as *Hylocomium alaskanum* and *Tomenthypnum nitens*. The shrubs *Betula nana* and *Salix pulchra* are also found, as is the dwarf-shrub *Dryas punctata*. Of the hygrophilous species, *Carex stans* remains longest of all, but later it too is replaced by *Carex ensifolia* ssp. *arctisibirica*.

In the forest tundra, even some trees (*Larix sibirica*) can grow on the rims of mires. High rims do not differ at all, with respect to vegetation, from the "zonal" communities with a closed cover. Even patches of bare ground can appear on them. The hygrophilous cover is preserved longest in the troughs which separate the polygons. They pass through the same stages of development as the central part of the polygons, only more slowly.

In the southern part of the zone, flat palsa bogs without polygonal cracking are more typical (Gorodkov, 1928; Boch, 1974; Tyrtikov, 1974, 1979). They generally consist of vast saturated depressions with sedge–moss vegetation and scattered nearly flat, almost round hummocks, 15–20 m across and 0.5–1 m high. The succession in the hollow proceeds in the same way as in the central parts of the polygons in polygonal mires. Because they are further south, palsa bogs in the terminal stages may include boreal species such as *Andromeda polifolia*, *Ledum palustre*, and *Rubus chamaemorus*. The appearance of hummocks is due to cryogenic processes in a saturated environment. They have a mineral core at their base. With the bulging of the ground, the moisture regime changes and the hydro- and hygrophilous species are gradually replaced by mesohygrophilous plants – that is, the change in cover is the result of changes in the environment. Hygrophilous mosses are replaced by *Dicranum angustum* and *D. elongatum* and by the liverwort *Tritomaria quinquedentata*. The sedges are substituted by the dwarf-shrubs *Vaccinium vitis-idaea* s.l. and *V. uliginosum* s.l.; then the shrub *Betula nana* becomes predominant. The stage of moss–birch community is long-standing and stable. With the moss cover becoming more compact due to the spreading of *Dicranum elongatum*, an intensive growth of peat can be observed. Then the acrocarpous moss *Polytrichum strictum* appears, forming a compact turf because of the presence of tomentum on the stem, which also aids in increasing the thickness of the turf. The hydrothermal conditions of the soil become worse due to heat insulation. The level of permafrost rises, and only the living part of the moss turf and the peat thaw out. The plant cover above the mosses becomes extremely sparse and impoverished, sometimes being restricted to 2–3 species. These include suppressed shrubs of *Betula nana*, solitary tussocks of *Eriophorum vaginatum*, and shoots of *Calamagrostis holmii*. The hummocks with a cover of *Polytrichum strictum* terminate the stage of development in an oligotrophic mire. The environmental conditions become so bad that even the moss turf begins to crack and die. Crustaceous lichens appear on its surface and the dead or dry turf is reduced to fragments. Ruptures appear in the fragmented turf and bare ground is uncovered. In this way, the succession of the hygrophilous sequence is completed, and in places frost-boil tundra can be formed in which the

overgrowth of bare ground proceeds in the same manner as on the "plakor".

A different type of peat hummock formation can be found up to the typical tundra subzone. These hummocks begin with the appearance in the depressions of small cushions of *Sphagnum squarrosum*. As the cushions grow and the moisture conditions change, *S. warnstorfii* appears and after a while dominates, sometimes with an admixture of *S. rubellum*. The latter is afterwards replaced by *S. fimbriatum* and *S. lenense*. At this stage, the height of the *Sphagnum* hummock is >25 cm. In summer, it does not completely thaw out; therefore, the process of decay in its lower part ceases. The *Sphagnum* mosses at the top of the hummock are later replaced by *Dicranum elongatum* and then by *Polytrichum strictum*. When the height of the hummocks reaches 30–35 cm, the natural replacement of various species comes to an end. The moss turf dies off from the surface, is covered with a film of liverworts and crustaceous lichens (*Coriscium viride*, *Mycoblastus tornoensis*, *Omphoria hudsonica*, *Ochrolechia inaequatula*), cracks, and begins to be destroyed. Such hummocks in the middle of a mire, dry, with flat surfaces and solitary vascular plants (*Calamagrostis holmii*, *Luzula confusa*, *Saxifraga cernua*, *S. nelsoniana*), are often chosen by birds as "canteens". The inflow of additional organic material in the form of bird excrement and lemming fecal pellets does not lead to any changes in the cover for a long time (only the bones of lemmings are overgrown with mosses such as *Aplodon wormskioldii* and *Tetraplodon mnioides*). The incoming organic material on hummock tops is generally not converted into a state suitable for the assimilation by autotrophic organisms. Therefore, such hummocks are destined only to be destroyed. In the High Arctic, turf hummocks are relatively short-lived because of an acute worsening of the hydrothermal conditions caused by their own development, again leading to their destruction.

In the arctic tundra subzone, mires are formed in hollows along the large ravines and in broadened river valleys (Gorodkov, 1956; Aleksandrova, 1963: Matveyeva, 1979a). The plants *Dupontia fisheri*, *Eriophorum angustifolium*, and *E. scheuchzeri* are early invaders and soon form a homogeneous and thick (60–80%) graminoid stand, 25–30 cm high. While the sedimentation of wet mud takes place under the action of snow and water erosion, these stands change only slightly. As soon as the erosion processes slacken, however, the surface of the mud is covered with mosses (*Bryum calophyllum*, *B. obtusifolium*, *Calliergon giganteum*, *C. sarmentosum*, *Campylium zemliae*, *Cinclidium arcticum*, *Drepanocladus intermedius*, *Mnium pseudopunctatum*), which stabilize it. Gradually, the moss cover becomes compact and there appear small herbs such as *Caltha arctica*, *Cardamine pratensis*, *Cerastium regelii*, *Chrysosplenium alternifolium*, *Juncus biglumis*, *Ranunculus sulphureus*, and *Saxifraga cernua*. The increase in the living part of the moss turf parallels the growth of peat below. This raises the turf surface, but, at the same time, causes the permafrost level to rise. In the graminoid cover *Carex stans* appears, in the moss cover *Drepanocladus revolvens*, *Tomenthypnum nitens*, and even *Hylocomium alaskanum*. The soil profile at this stage of mire formation is simple: 6–8 cm of living plants; up to 15–20 cm of peat; and lower, down to the permafrost, a gley horizon. Peat hummocks may appear within such valley mires. Their formation begins with cushions of *Sphagnum*, or if it is absent from the flora, of *Aulacomnium turgidum*. In the northern part of the tundra zone, such hummocks are short-lived because of the thermal insulating properties of the peat-moss turf.

The sedge–moss stages can persist for a long time. If a lowering of the erosion base level takes place, the hydrological conditions will change towards drainage. The hydrophyte mire succession will be completed and the stage will be set for the formation of frost-boil communities.

Overgrowth of mud banks

The large mud banks along the shores of river estuaries begin to be overgrown when the area ceases to be strongly influenced by the sea tides (Gorodkov, 1956). On aerated rusty mud deposits and on dove-gray mud deposits smelling of hydrogen sulfide, the first to settle are the blue-green algae (*Gomphosphaeria* sp., *Merismopedia glauca*, *M. punctata*, *Nostoc coeruleum*, *Phormidium autumnale*). The surface dries up during summer and is cracked into polygons. Then overgrowth of the dried mud begins, first by *Puccinellia phryganodes* and then by a film of small mosses (*Bryum arcticum*, *B. nitidulum*, *Distichum hagenii*, *Pottia heimii* var. *obtusifolia*). When sedimentation and soil salinization decrease, the cover of *Puccinellia phryganodes* closes up and small patches of *Carex*

ursina, *C. subspathacea*, *Dupontia psilosantha*, and *Stellaria humifusa* are interspersed within the mat.

The vegetation from the water edge to areas which are not flooded during severe storms presents both an ecological and a successional sequence. As the distance from the water's edge increases, more advanced successional stages are encountered.

In this biotope, endodynamic successional processes cannot lead to the formation of more mature phases of the vegetation if there are no changes in the ecological conditions. Thus, a thick cover of *Puccinellia phryganodes* can be formed only when active sedimentation has ceased. Soil is formed parallel to the development of the plant cover. At first, a dark-brown horizon of peat (A_0) appears fragmentarily under the solitary tufts, under which, down to the very permafrost (at 50–70 cm), a wet gley of grayish color with rusty spots is to be seen. The soil is unevenly salinized; in places, it effervesces carbon dioxide and hydrogen sulfide. Decomposition is severely retarded by the hydrothermal conditions in the soil, so that the soil contains a large quantity of dead preserved roots. Outside the sedimentation zone, where salinity is also less, *Puccinellia phryganodes* is replaced by *Dupontia fisheri*. The *Dupontia* communities remain essentially unchanged until the hydrological conditions have changed towards drainage, when an enrichment of floristic composition occurs with species such as *Alopecurus alpinus*, *Caltha arctica*, and *Eriophorum scheuchzeri*. A thin layer of the mosses *Bryum calophyllum* and *Calliergon giganteum* is formed. Further development of such communities is similar to successions on the ravine bottoms and widened parts of river valleys.

Overgrowth of small and shallow pools on the sites of thermokarst depressions proceeds by the development of the mosses *Calliergon giganteum*, *C. sarmentosum*, *Campylium zemliae*, *Drepanocladus lapponicus*, *Scorpidium scorpioides*, and *S. turgescens*, which are either fastened to the bottom or form a quagmire. At the same time in the north, grasses (*Arctophila fulva*, *Dupontia fisheri*, *Pleuropogon sabinei*) and forbs (*Caltha arctica*) begin to grow in shallow waters; in more southerly regions, the species *Hippuris vulgaris* and *Ranunculus palassii* appear. Gradually, the humus of dead mosses becomes more compact, filling in the space and forcing out the water. The water-basin stage of succession is replaced by a mire stage (Gorodkov, 1956), a small sedge–moss or moss-peat hummock may be formed. When they are destroyed, the formation of "zonal" tundra begins.

Animal communities in wetlands

Hydromorphic communities represent different stages of various succession rates with great variations in their biodiversity, biomass, and productivity, which distinguish them significantly from climax "zonal" communities. This is well illustrated by the animal assemblages of the wetlands. The inhabitants, hydrophilous organisms, form a considerable part of the arctic fauna, and in many taxa the proportion of hydrophilous species is substantially higher than in more southerly biomes. For example, the most diverse and numerous groups of Diptera in the Arctic have their larvae in water or in hydromorphic terrestrial communities: Chironomidae, Culicidae, Limoniidae, Mycetophilidae, and Tipulidae. Tipulid larvae of the genus *Prionocera* are the most important inhabitants of the wet moss layer. Together with large usually highly pigmented worms of the families Enchytraeidae and Lumbriculidae, they form the bulk of the zoomass in mires. Many Collembola species (within *Hypogastrura*, *Isotomurus*, *Podura*, etc.) are also very abundant in various hydromorphic biotopes. Sometimes freshwater hoppers (Gammaridae) and shield-bearing phyllopods (Notostraca) become very abundant in wet moss. In southern tundras, molluscs are still numerous. The proportion of hydrophilous forms is also great among arctic birds. Everywhere the "bog" species of sandpiper (*Calidris acuminata*, *C. alpina*, *C. melanotos*, *C. minuta*, *Phalaropus phulicarius*, *Philomachus pugnax*, etc.) are among the main dominants in bird populations. Besides typical hydrophilous forms, many mesophilous groups, such as earthworms, ground beetles, rove beetles, etc., also inhabit mires. All of this characterizes the bog communities as typical "intrazonal" elements of the landscape.

Different types of tundra mires are populated by a wide range of animal groupings that differ in biomass, faunistic density, and ecological composition (Chernov, 1978b). The animal communities of polygonal mires have a highly complex structure (Chernov, 1961, 1973a). The following groups may be distinguished: (1) the communities of hollows in the polygons, which are dominated by hydrophilous enchytraeids and tipulid larvae; (2) the communities of wet slopes of the rims with a small

zoomass, but a rich faunistic composition; and (3) the communities of drier rim tops which by their faunal composition correspond to those in moss tundras (here the soil layer is populated mainly by *Eisenia nordenskioldi*, which provides the bulk of the zoomass). In mires, it is in the peat hummocks that many animals, and particularly the pupae of insects inhabiting the hollows, survive the winter period. Many dipterans migrate to the peat hummocks for pupation – for example, *Conosyrphus tolli*, *Helophilus borealis*, *H. groenlandicus*, and many Muscidae.

The total zoomass of a mire normally does not exceed 15 g m^{-2} (on average it is about 10 g), although at intermediate stages of development of the mire communities a relatively high biomass may be developed (Table 16.22). Sometimes the faunistic composition of these groups is very poor, for example, in small thermokarst mires which are inhabited mainly by 1–2 species of hydrophilous enchytraeids and sandhoppers, giving a zoomass of up to 30–40 g m^{-2}. Sometimes, on the other hand, it is very rich, combining meso-, hygro-, and hydrophilous forms — for example, the animal population at some initial stages in mire formation on terraces. The zoomass may then increase to 200 g m^{-2}, with a very diverse faunistic composition (Chernov, 1961, 1964). An important feature of the animal population in different types of mires is the sharp variation in main indices, especially in total biomass. These fluctuations are apparently due to the stage of mire development, its location in the relief, the peculiarities of the underlying ground, and so forth.

Formation of meadows on south-facing slopes

Vegetation of a meadow type (Figs. 16.63, 16.64), with a predominance of mesophilous grasses and forbs, is formed in places where there is enough heat and no excess of moisture. In the tundra zone where the index of dryness (Budyko, 1956) is about 0.3, the herbs can successfully compete with mosses and dwarf-shrubs only on south-facing slopes. Though a southerly aspect is favorable for the development of meadows, it is not sufficient. The slope also must be of a certain steepness. On slopes which are too steep, erosion interferes with the process of overgrowth and the vegetation is retarded at the earliest stages of the

TABLE 16.22

Population (m^{-2}) of hydrophilous invertebrate mesofauna in various regions of the Arctic[1]

Group	Wet marshes		Wet basins in polygonal mire (Taymyr)		Rim in polygonal mire (Taymyr)	Thermokarst water pool on snowbed (Taymyr)	Graminoid moss stand influenced by melting water of snowbed
	Anabar Bay	Yamal	Agapa river	Tareya	Agapa river	Anabar Bay	Anabar Bay
Annelida: Oligochaeta (Enchytraeidae and Lumbriculidae)	140	190	320	292	200	76800	7680
Arthropoda							
Crustacea: Amphipoda (Gammaridae)	20	30	0	0	0	23	0
Insecta: Coleoptera							
Carabidae	4	2	0	2	6	0	3
Staphylinidae	7	19	4	0	4	190	135
Insecta: Diptera							
Larvae of Tipulidae and Limoniidae	68	72	3	29	3	128	91
Other Diptera	21	125	11	80	43	48	98
Total zoomass (g fresh weight m^{-2})	14	17	6	10	7	230	210

[1] From Chernov (1978b).

Fig. 16.63. Herb–grass meadow on a southern slope in the southern tundra subzone at Kresty, Taymyr. In the background is a northern slope with a dwarf-shrub stand.

succession with a few pioneer species. On too-gentle slopes, the combination of heat and moisture becomes almost the same as on the "plakor". Then, at the earliest stages a moss cover is formed and the succession follows the "tundra" type. The optimal steepness of slope for the formation of meadows is 30–40°. A sufficient snow depth in winter, melting quickly in spring, is also necessary. The formation of a meadow on eroded sections of southern slopes begins with the establishment of pioneer species, mainly of forbs (*Artemisia tilesii*, *Descurainia sophioides*, *Draba hirta*, *Polemonium boreale*, *Taraxacum ceratophorum*, *Tripleurospermum phaeocephalum*). Their cover gradually becomes thicker. Then, the slopes are invaded by new species typical for later stages of succession. A stable grass stand is made up of a large number of species (up to 70 in one community), 10–15 of which are highly abundant. The commonest species in the tundra meadows are the grasses *Alopecurus alpinus*, *Festuca brachyphylla*, *F. cryophila*, *Koeleria asiatica*, *Poa alpigena* and *Trisetum sibiricum* and the forbs *Astragalus subpolaris*, *A. umbellatus*, *Campanula langsdorffiana*, *Cerastium maximum*, *Dianthus repens*, *Hedysarum arcticum*, *Myosotis asiatica*, *Pachypleurum alpinum*, *Pedicularis verticillata*, *Polemonium boreale*, *Polygonum bistorta* (*Bistorta major*), *P.* (*Bistorta*) *viviparum*, *Potentilla stipularis* and *Valeriana capitata* (Matveyeva et al., 1973; Chernov and Matveyeva, 1979; Matveyeva and Zanokha, 1986, 1993).

Tundra meadows on south-facing slopes are stable because of a number of factors. First of all, erosion processes caused by cryogenic phenomena are constantly occurring on the slopes. The soil cracks and slips down the slope. As a result, new bare patches of ground are formed which are again populated by pioneer herbs. In other words, the endogenic succession is permanently impeded by the instability of the soil, and the succession cycle is repeated locally. Secondly, the herbs successfully compete with mosses and prevent the latter from forming a thick turf. Usually on the soil, under a thick cover of herbs, only small cryptogam species survive in a suppressed state and form a very thin (to 0.5 cm) discontinuous film. Dwarf-shrubs also cannot grow well under a thick cover of herbs. Although *Dryas* does form the lower layer in herb

Fig. 16.64. Herb meadow with *Polygonum bistorta* (*Bistorta major*), *Cortusa matthioli*, and *Taraxacum macilentum* on the southern slope of the bank of the Rogozinka River in the typical tundra subzone in western Taymyr (about 73°N).

communities, the vitality of the specimens is reduced and they form no flowering shoots. Thirdly, the south-facing slopes are places with high lemming activity. On the one hand, these animals loosen the soil and aid in its aeration, drainage, and erosion. On the other hand, they fertilize the soil. All this taken together helps the herbs to flourish. Earthworms and other soil invertebrates, which are abundant here, contribute to the increase in soil fertility in these biotopes (Chernov, 1978b). The result of the combined action of all biogenic and abiogenic factors is a specific succession leading to the formation of a particular type of plant cover in meadows different from that of the tundra proper (Tikhomirov, 1946).

It is interesting to note that the tundra meadows on south-facing slopes are most frequent in the middle part of the tundra zone (Chernov, 1978b, 1980). In southern tundra and in forest tundra, in spite of a more favorable climate, pure herb communities are rare. They always contain many shrubs (willows, birches), which are the most active component of the vegetation. In essence, such mixed communities represent a more advanced stage of succession which is not reached in the typical tundra subzone. In the southern part of the zone, the shrubs quickly replace the meadow stages, which are of short duration there. This process can be compared with shrub development in meadows of temperate belts if they are not subjected to pasture or hay-making.

To the north in the arctic tundra subzone, there is so little heat that even in the most favorable microclimate on south-facing slopes meadows can-

Fig. 16.65. Fresh one-day-old landslide by the Rogozinka River in Taymyr, August, 1984.

not develop. There are reasons to believe that at the northern border of the tundra zone, the formation of mesophytic herb communities is possible only with the participation of lemmings. In the arctic tundra subzone, the forb–grass groupings on south-facing slopes are made up of species quite common in "zonal" communities: *Alopecurus alpinus*, *Draba glacialis*, *D. subcapitata*, *Eritrichium villosum*, *Luzula confusa*, *Papaver polare*, *Pedicularis oederi*, *Saxifraga caespitosa*, *S. hieracifolia*, *S. hirculus*, *Senecio resedifolius*, and *Stellaria ciliatosepala* (Zanokha, 1995).

There are no meadows in polar deserts (Matveyeva and Chernov, 1976; Matveyeva, 1979b).

From a dynamic point of view, meadows in the tundra zone can exist for a long time only with an optimal combination of heat and moisture (differing from the conditions of "plakor") – that is, only in the middle part of the zone. The meadow stage in the south, as mentioned, is quickly replaced by the shrub stage, while in the north it is only found with the addition of organic material from animals.

Overgrowth of landslides

All the successions described above proceed extremely slowly, and even prolonged observations seldom give the opportunity to notice any essential changes. Therefore, the plant cover appears to be quite stable. The vulnerability and instability of the tundra cover is especially distinct at times of catastrophic destruction as a result of landslides, when huge masses of soil together with vegetation slip down the surface of the permafrost (Fig. 16.65). This takes place during short periods of time: within minutes or a few hours. The overgrowth of landslides extends over many years. It is especially slow on steep slopes where new masses of soil melt off and slip down for a long time.

The overgrowth begins when the surface is smoothed out, dried, and stable, even if only for a short time (Matveyeva, 1979a). Vascular plants become established on such surfaces, the first of which include grasses (*Alopecurus alpinus*, *Deschampsia glauca*, *Poa alpigena*, *Puccinellia angustata*) and some forbs (Fig. 16.66). The most active of the pioneer mosses on landslides are *Bryoerythrophyllum recurvirostre*, *Ceratodon purpureus*, *Funaria hygrometrica*, *Pohlia nutans*, and *Pottia heimii* var. *obtusifolia*. In moist places, the

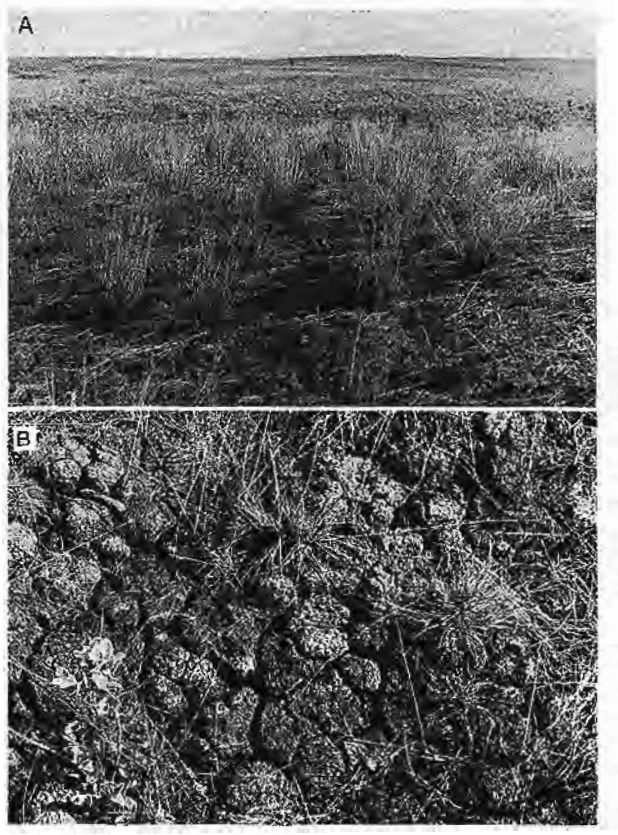


Fig. 16.66. Landslide being overgrown with *Deschampsia glauca* by the Rogozinka River in Taymyr. A, general view; B, ground surface.

liverworts *Anthelia juratzkana* and *Gymnomitrion corallioides* are abundant. After the formation of the first relatively stable grass–forb cover, succession depends on the substrate and moisture status. At the terminal stage, the original vegetation may be restored, but it is difficult to determine the time required for this.

Influence of animals on vegetational succession

The lemmings (*Dicrostonyx torquatus*, *Lemmus sibiricus*) influence tundra vegetation more than any other animals because of their abundance, in particular in years of increased numbers (for details see pp. 113–116). Their influence is twofold: through the removal of green biomass from the ecosystem on the one hand, and through changes in the physical and chemical state of the substrate due to loosening and fertilizing by excrement on the other. In winter, they live in wetlands. Using the lower parts of plants for their food, lemmings detach a great amount of dry parts of grasses (*Arctophila fulva*), sedges (*Carex stans*) and cotton grasses (*Eriophorum angustifolium*, *E. vaginatum*), which fall on the surface as a hay (see Fig. 16.88). Most of this "hay" is carried away by melting water, out of the community which produced this organic matter. Both the speed of natural succession and its direction are changed by the removal of litter, because litter accumulation leads to a worsening of the hydrological regime and the general environment for vascular plants. The input of organic matter in the form of excrement increases the fertility of poor bog soil. Thus, lemmings partly change the direction of succession due to the eutrophication of the substrate and reduce litter accumulation. Their main role is in the stabilization of the ecosystem. On the outskirts of vast mire depressions where lemmings make their holes, the vegetation cover can be noticeably changed. The eutrophic shrub willow *Salix lanata*, a moss cover of *Bryum*, *Cinclidium*, and *Mnium*, and the forbs *Polemonium acutiflorum*, *Rumex arcticus*, *Saxifraga cernua*, *S. nelsoniana*, and *Valeriana capitata* are typical of such places instead of sedges, cotton grasses, and the mosses *Calliergon*, *Drepanocladus*, and *Sphagnum*.

In spring, lemmings move to better-drained environments, mainly to the south-facing slopes. The very existence of herb and grass meadows on south-facing slopes is due to the combination of southern exposure with additional heat and lemming activity which loosens and fertilizes the soil (Aleksandrova, 1956; Tikhomirov, 1959; Chernov, 1978b, 1980). In the arctic tundra subzone, these latter processes play a highly significant role, and the meadows are mainly of zoogenic origin. If lemmings inhabit nearly flat sites in "zonal" communities, then the vegetation cover changes completely. Patches of dense herb cover with *Draba glacialis*, *Myosotis asiatica*, *Poa alpigena*, *P. arctica*, *Saxifraga cernua*, and *S. hirculus* are formed.

On fresh landslides, where earlier frozen marine deposits have been uncovered and no soil has been formed, there are usually only isolated individuals of some grasses (*Alopecurus alpinus*, *Deschampsia borealis*, *Poa alpigena*, *Puccinellia angustata*). However, when there is a lot of lemming excrement on these landslides, the same species form a very dense cover with bright green foliage.

The voles *Microtus middendorffii* and *M. gregalis* are widely distributed in the southern half of the tundra zone. In the regions where they are abundant (in northeastern Europe), they also significantly change the vegetation (Dunaeva, 1948). Mesophilous forbs and grasses become more abundant on slopes with large vole colonies. Such places can already be clearly seen in spring: the green color of early grass growth against the background of gray-brown tundras.

In the northeastern sector of the Eurasian Arctic to the east of the river Kolyma, another rodent, the long-tailed Siberian suslik (*Citellus undulatus*), exerts influence on the tundra vegetational succession. The composition of herb communities near suslik holes is the same as near those of the arctic fox or voles; additional species include *Aconitum delphinifolium*, *Androsace septentrionalis*, *Bromopsis pumpelliana*, *Calamagrostis purpurea*, *Corydalis sibirica*, *Phlox alaskensis*, *Polygonum laxmanii*, *Pulsatilla multifida*, *Ranunculus affinis*, and *Veratrum oxysepalum*.

The reindeer (*Rangifer tarandus*) is the only abundant species of large herbivorous mammals in Eurasian tundras. In spite of its high numbers in some tundra areas during summer and its comparatively large withdrawal of primary production from the ecosystems, this animal has no strong influence on vegetation. This is due to such special features in biology and behavior of the wild form of reindeer as seasonal migration. The influence of a reindeer herd is difficult to notice even immediately after grazing. Only wild reindeer can successfully utilize a wide range of low productive pas-

tures without causing any real damage to the vegetation and without changing the natural succession. The domesticated populations of reindeer, which are grazed in a limited area, are more dangerous for the plant cover (Kryuchkov, 1979), especially for winter lichen pastures. Under intensive winter grazing, these pastures are completely degraded in 3–4 years and are replaced by grass or sedge communities. The lichens (*Cladina stellaris*) begin to grow actively only 6 years after grazing has ceased. For the complete restoration of a winter pasture, 15–20 years are necessary. Winter pastures of domesticated reindeer, however, are situated mainly in the northern taiga outside the southern limit of the tundra zone.

The influence of the arctic fox, *Alopex lagopus*, is local, but very strong. Foxes usually make their holes in low hills, in steep slopes with sandy loam. Because of the deep passages with many entrances, the arctic fox promotes permafrost thawing to a great depth as well as soil aeration. In addition, the soil surface is constantly being fertilized by their excrements. Arctic fox holes are easily seen from a distance because of the luxuriant vegetation around them, which contrasts with the surrounding tundras (V.N. Andreyev, 1932; Aleksandrova, 1956; Tikhomirov, 1959). Whatever the original vegetation may have been, it is replaced by a dense cover of grasses (*Alopecurus alpinus*, *Calamagrostis holmii*, *Koeleria asiatica*, *Poa alpigena*, *Trisetum spicatum*) and forbs (*Artemisia tilesii*, *Cerastium maximum*, *Descurainia sophioides*, *Draba hirta*, *Lloydia serotina*, *Oxyria digyna*, *Parrya nudicaulis*, *Polemonium boreale*, *Ranunculus borealis*, *Stellaria ciliatosepala*, *Taraxacum macilentum*, etc.). It is a sort of permanent pioneer cover due to the constant activity of adults and especially young animals. The plant cover is locally continuous, but it has an obvious mosaic structure because of the vegetative spread of some species. All plants are in a good state. They have considerable green biomass and produce a large amount of good-quality seeds. Grass–forb vegetation may exist near holes for hundreds (and perhaps thousands) of years; however, with regard to dynamics, these are the initial stages of a succession which is permanently interrupted as a result of the animals' activity. The holes in the hill and the resulting absence of permafrost lead to a good aeration and soil warming. Fertilization by excrement increases the soil fertility. All this gives the grasses a chance to compete successfully with mosses.

The influence of birds is mostly noticeable where they feed. As in the case of reindeer, geese (*Anser albifrons*, *A. fabalis*) do not significantly damage the vegetation cover because they have large feeding areas. Birds of prey, on the other hand, come to the same local sites for many years to eat their victims. Owls (*Asio flammeus*, *Nyctea scandiaca*), falcons (*Falco peregrinus*), rough-legged hawks (*Buteo lagopus*), and skuas (*Stercorarius longicaudus*, *S. parasiticus*, *S. pomarinus*) all change the vegetation cover locally in feeding places. For their "canteens", these birds select the upper parts of the relief in two different types of environments. Falcons and hawks prefer the tops of rocks or high snowless hills, while owls sometimes use the ledges of steep river banks. Whatever the vegetation in such places had been before (even if they were without plants), it is replaced by a dense cover of *Calamagrostis holmii* and *Poa arctica* with some forbs (*Draba hirta*, *Cerastium maximum*, *Potentilla hyparctica*). The soil is also radically changed. Even on a stony substrate used for many years as a "canteen", a layer of humus and peat 0.3–0.8 m thick is formed. The skuas and owls have their meals, rest, and seek their prey on the peat-moss hummocks among the mire depressions. The moss turf becomes compact with a dominance of *Dicranum congestum*, *D. elongatum*, and *Polytrichum strictum*. The even and "solid" surface of the moss turf is covered by a thin film of crustaceous lichens and liverworts. Solitary vascular plants (*Calamagrostis holmii*, *Luzula confusa*, *L. nivalis*, *Poa arctica*, *Saxifraga cernua*, *S. foliolosa*) can grow there, but they all are suppressed. The lemming pellets become overgrown by mosses such as *Aplodon wormskioldii* and *Tetraplodon mnioides*.

On small islands in the tundra lakes, taken over by colonies of seagulls, the native vegetation cover is completely exterminated. Surplus organic matter in the form of bird droppings reduces the plant cover severely. Usually only *Senecio congestus* dominates and forms a thick vegetation cover about 1 m high. On the rocks around bird colonies, dense thickets of nitrophilous plants are typical. Species including *Draba cinerea*, *Polemonium boreale*, *Puccinellia angustata*, *Rhodiola borealis*, and *Saxifraga cernua* are usually much larger than in any other environment.

In general, the influence of vertebrates on the dynamic processes in tundra vegetation consists in the following: grazing of plants (by reindeer, geese,

and rodents), fertilization (by all animals), loosening of soil (by arctic fox and rodents), and damage to plants and partly to soil cover (by reindeer, geese, and rodents). In the majority of cases, the animal activity slows down the rate of natural succession, often changes its direction radically (for instance towards meadow formation), and can also cause erosion. Almost all forms of influence are of local significance, but lemming activity is important at the landscape scale.

Changes in tundra vegetation under the impact of man

The composition and structure of vegetation cover in the tundra zone, as well as the rate of recovery after human impact, depend on many factors, such as the character and the extent of the disturbance, the period for which this factor was in action, the period of recovery, and the resources of local flora, which vary in different subzones and regions of the tundra zone (Matveyeva et al., 1973; Druzhinina and Zharkova, 1979; Matveyeva, 1979c, 1988a; Yurtsev and Korobkov, 1979; Druzhinina, 1985; Korobkov, 1985; Matveyeva and Zanokha, 1986; Sumina, 1994). The multiplicity of these factors and their combination give great variety to the process of vegetation restoration, but the general tendency of this process can be traced for the whole tundra zone.

The restoration of natural plant cover everywhere in the tundra depends on the local flora resources. The numbers of adventive species can be rather large in the vicinity of towns and settlements in the southern part of the tundra zone – for instance, there are about 90 plant species of this category in the Vorkuta region (Dorogostayskaya, 1972; Druzhinina, 1985) – but their role in succession is not great. Introduced species invade the tundra in different ways. They are either naturalized cultivated plants or brought into an area as food or fodder. Only very few introduced plants are able to become acclimatized in the Arctic for a prolonged period of time. More often they grow in local biotopes for some time without producing good-quality seeds and then die out. The naturalization of certain introduced plants takes place only in the southernmost regions of the tundra zone — for example, *Artemisia vulgaris*, *Plantago major*, *Polygonum aviculare*, *Stellaria media*, *Trifolium repens*, and *Urtica dioica*. Species such as *Agropyron repens*, *Capsella bursa-pastoris*, *Chenopodium album*, *Rumex confertus*, *Stellaria media*, and *Thlaspi arvense* may be active in the initial stages of the anthropogenic successions, but only very few species succeed in remaining established for a long time in disturbed places in northern Eurasia. This is the case for *Matricaria matricarioides*, an American species that was brought to the Vorkuta region, where it has spread intensively and sometimes formed a dense vegetation cover. Most adventitious species, however, occur even in the southern tundra only as a result of frequent reintroductions. In the northern parts of the Arctic, there are no such species at all.

The resources of the local flora are rich enough for a natural restoration of the vegetation. More than half of the local flora can be observed in disturbed sites, but only about 30–40 species play an active role in this process in every region. Most abundant in environments disturbed by man are species which in natural conditions grow on eroded slopes, landslides, screes, on river and brook banks, as well as on zoogenic biotopes. Rootstock and bunch grasses and forbs (mainly tap-rooted) predominate. All of these species are nitrophilous and associated with eroded surfaces. The species vary depending on the latitude and longitude of the area, although some are active throughout the tundra zone: *Arctagrostis arundinacea*, *Artemisia tilesii*, *Astragalus subpolaris*, *Calamagrostis holmii*, *Chamaenerion angustifolium*, *Cochlearia arctica*, *Deschampsia glauca*, *Descurainia sophioides*, *Equisetum arvense* spp. *boreale*, *Pedicularis verticillata*, *Poa alpigena*, *P. arctica*, *Polygonum* (*Bistorta*) *viviparum*, *Senecio congestus*, and *Tripleurospermum phaeocephalum*.

The main ways in which the tundra vegetation is disturbed are the mechanical destruction of the plant mats by different types of vehicles and the compression of the mats as a result of trampling. If the plant cover has been destroyed completely but without destruction of the upper soil layer, then the usual course of succession is by formation of a meadow. This process can be observed around settlements, near hunters' huts, near traps for the arctic fox, on old graveyards of native people, and on heavily used vehicle tracks after the traffic has stopped. The composition and structure of newly formed communities are quite different from the natural ones. The main tundra dominants like mosses, lichens, dwarf-shrubs, and shrubs normally disappear, while grasses and forbs become abundant. The number of species in anthropogenic

meadows is only one-third to one-half that in the natural tundra meadows on south-facing slopes. They have a mosaic horizontal structure due to the spreading of some species which are able to form pure stands. These include *Artemisia tilesii*, *Cerastium maximum*, *Chamaenerion angustifolium*, *Polemonium boreale*, *Pyrethrum bipinnatum*, *Stellaria ciliatosepala*, *Taraxacum ceratophorum*, and *Tripleurospermum phaeocephalum*. The restored plant cover is more productive than both "zonal" tundra communities and natural tundra meadows. For example, the annual aboveground productivity of vascular plants is 68 g m^{-2} (air-dry weight), in "zonal" communities on Taymyr, 217 g m^{-2} in natural meadows on south-facing slopes, and as much as 450 g m^{-2} in anthropogenic meadows (Chernov et al., 1983). The densest and most productive grass stands are usually formed in the vicinity of small settlements of fishers and hunters, where, along with the tearing and compression of the vegetation cover, a great amount of organic matter in the form of garbage may be mixed into the soil. The addition of nitrogen is a factor that stimulates the vitality and productivity of grasses. The composition of such grass stands is similar to that around arctic fox burrows and in sites subject to intense lemming activity.

The anthropogenic meadows are rather stable, with the composition and structure remaining the same for long periods (more than 20 years). This indicates that, under the present climatic conditions, nitrogen top-dressing may encourage successful competition of grasses with mosses, which are the main antagonists in the tundra. We do not as yet have any examples of the complete restoration of natural vegetation cover of "zonal" communities in places where anthropogenic meadows are formed. "Zonal" tundra communities are subjected to man's impact more than any other types of tundra vegetation because they occupy just those areas that man chooses for his settlements, buildings, and transport.

Where plant cover has been disturbed by vehicles in saturated environments, recovery usually involves *Arctophila fulva*, *Carex stans*, *Eriophorum angustifolium*, and *E. scheuchzeri*. Since these are the same species that had grown there before, the difference between natural communities and those caused by man's activity is less than that between dwarf-shrub–sedge–moss tundras and grass meadows.

If the natural cover is not destroyed completely and its structure is preserved, for example after a few occasional passages of vehicles, some grasses (e.g. *Alopecurus alpinus*, *Arctagrostis latifolia*, *Deschampsia glauca*, *Poa alpigena*) usually become more abundant, but they do not form a dense cover. If vehicle movements are not repeated, the initial vegetation recovers, although the tracks can still be seen for a very long time.

The regeneration of vegetation is particularly impeded on coal heaps and oil pools. These spots remain lifeless for a long time. Only isolated species can survive there, but eventually even these will perish.

Fires started by man lead to the destruction of natural tundra vegetation, but have no such catastrophic effects as in forests or steppes. Fires occur episodically near the southern tundra border, mainly in the forest tundra and very rarely in the southern tundra subzone where they are always local. The restoration of vegetation proceeds along the same lines as in the case of mechanical disturbance. Additional mineral fertilizer in the form of ash promotes more rapid grass growth and leads to better vitality and higher productivity (Polozova, 1986).

Anthropogenic pressure becomes most dangerous when the whole dynamic system vegetation–soil–permafrost is disturbed. The vegetation cover and the permafrost are components of a single system in a state of equilibrium. The stability of this equilibrium reflects the orderly structure of the tundra landscape. Destruction of the vegetation cover, for example when building and traffic movements in summer become too intensive in places with high ice content in the soil and particularly where there are ice lenses, may be the cause of thermokarst processes which result in the formation of ravines, landslides, and small pools. In these cases, the anthropogenic pressure is the reason not only for vegetation changes, but also for irreversible landscape destruction (Kryuchkov, 1976, 1979). Under the action of meltwater and rain, the unfrozen soil slips down to the depression over the permafrost surface.

Primary succession starts on Quaternary marine sediments without any signs of soil formation. This is analogous to natural landslides. If there is no addition of organic matter, such areas remain in the earliest stages of succession for many years. Just as on landslides, isolated specimens of a few species grow there without forming anything like a closed cover. The following species are the most

typical for such sites: *Alopecurus alpinus*, *Cochlearia arctica*, *Deschampsia glauca*, and *Puccinellia angustata*.

Biotopes influenced by man can be divided into two groups. The first group includes biotopes where the environment worsens under human impact — in extreme cases, when the soil cover is destroyed completely. This type is analogous to erosion-generated landslides, which are very typical for the tundra zone. Species of such naturally disturbed biotopes play a main role in the restoration of the vegetation cover in the anthropogenic habitats. Sites polluted by oil and coal may be included in this first group. There are no natural analogues to these biotopes. The very slow restoration of plant cover is performed by a few pioneer species. For example, *Arctagrostis arundinacea* forms a highly productive, closed stand on former coal heaps. In this group of anthropogenic habitats, the unfavorable tundra conditions become very extreme and are the reason for the very low succession rate, prolonged persistence of the initial stages, and the poor species composition.

The second group includes human-influenced biotopes where the whole ecological situation improves when compared to natural conditions. Mechanical tearing-up of the plant turf, especially the moss cover, leads to better soil warming, deeper thawing of the permafrost, and better drainage and aeration. This speeds up decomposition and finally makes the poor tundra soil more fertile. Addition of organic matter in the form of garbage has an even more marked effect. The environmental conditions in such habitats are optimized and become more similar to those of the temperate belts. The biotopes analogous to this group of human-influenced habitats are the south-facing slopes and the zoogenic biotopes in the tundra. Typical species for these communities are also the main components of human-influenced meadows, which can be formed under the action of organic matter without mechanical damage of the natural cover. Adventitious species can mainly survive in this second group of anthropogenic habitats.

The environments of these two groups occupy each end of the environmental gradient. The biotopes of the second group are most interesting because the competitive interrelations between species are changed. The "violent" (aggressive) species (Ramenskyi, 1938) of the natural tundra communities, well adapted to cool, wet soils short of nitrogen, are replaced by species that are "patient" (subordinate) in the tundra conditions. When the conditions are artificially changed to the ecological optimum of the subordinate species, they become aggressive. In "zonal" tundra communities, where the main dominants are mosses, lichens, and dwarf-shrubs, the annual aboveground production is very low. Most parts of plants remain alive for many years. In the anthropogenic meadows where grasses and forbs predominate, the whole aboveground phytomass becomes litter in one or two years. This is why the anthropogenic meadows, where the turnover is more intensive than in natural tundra communities, prove to be very stable self-maintaining systems.

The meadow stage in the anthropogenic succession after disturbance of "zonal" tundra is analogous to that in the temperate belts after the removal of forests. For the reasons mentioned above, they can exist for a considerable length of time without restoration of natural plant cover even if human disturbance is not repeated (Fig. 16.67).

Human influence in the tundra zone does not reach such tremendous scales as in many regions of the temperate belts. The sites intensively changed by man are in the vicinity of settlements, which are not so numerous in the tundra zone, especially not in more northerly areas.

Scientists working in the tundra very seldom use the term "weed", although they do describe human-influenced stands. The species forming these communities are met only or mainly in human-influenced stands; although the following species have had their distribution areas widened over the tundra zone under human activity: *Arctagrostis arundinaceae*, *Artemisia tilesii*, *Cerastium regelii*, *Cochlearia arctica*, *Deschampsia sukatchevii*, *Descurainia sophioides*, *Koenigia islandica*, *Phippsia algida*, *Ranunculus hyperboreus*, *Stellaria humifusa*, *S. crassifolia*, and *Tripleurospermum phaeocephalum* (Dorogostaiskaya, 1972; Matveyeva, 1979c; Yurtsev and Korobkov, 1979; Sumina, 1994). Over the past 20–30 years, some of these species in the native tundra flora have been acquiring the status of weeds. This has not previously happened in the tundra, although in all other biomes mankind has been faced with this problem for hundreds or even thousands of years.

It should be stressed that tundras are very fragile natural ecosystems. They can easily be destroyed and their restoration requires a very long time. There are very few types of anthropogenic commu-

Fig. 16.67. Anthropogenic vegetation on the foundations of an old house in the southern tundra subzone at Kresty, Taymyr.

nities in the tundra zone, and these few are floristically much poorer than the natural communities. Thus, in high latitudes human activity leads to a drastic lowering of an already poor biotic diversity. If human impact takes place on a similar scale in the tundra as in more southerly regions, it will lead to the appearance of poor, dull and monotonous landscapes. And as is well known to ecologists, the resistivity of nature depends on its diversity.

Different groups of plants in dynamic processes

One of the most important functions of plants at early stages of succession is the stabilization of the ground surface, because the arctic organisms are constantly being destroyed by cryogenic processes. Plants of different systematic and ecological groups make their home on the surface of unstable ground as the first settlers. They are mainly green and blue-green algae, crustaceous lichens, small liverworts, and bryoid mosses. Their survival is possible because of their small size and peculiarities of metabolism and morphology which ensure their relative independence of the environment (ability to survive unfavorable periods by lowering metabolism, passing over to anabiosis, long-term existence as spores, possibility of functioning with minimum reserves of available nutrients, absence of root systems, and ability to break contact with the substrate). In different regions of the Arctic, the taxonomic composition of these organisms is relatively similar. The most widely distributed are the following groups and species: algae of the orders Oscillatoriales and Chlorococcales; crustaceous lichens (primarily within the genera *Baeomyces*, *Bilimbia*, *Lecanora*, *Lecidea*, *Ochrolechia*, *Pannaria*, *Pertusaria*, *Psoroma*, *Rinodina*, *Toninia*); liverworts (e.g., *Anthelia juratzkana*, *Gymnomitrion corallioides*, *Odontoschisma denudatum*, *Peltolepis grandis*, *Solenostoma pusillum*); and bryoid mosses (e.g., *Ceratodon purpureus*, *Distichum capillaceum*, *Ditrichum flexicaule*, *Funaria hygrometrica*, *Myurella julacea*, *Psilopilum laevigatum*). These small autotrophic organisms perish, but a thin crust of organic material is gradually formed on the ground surface by their living and dead parts. This thin organic crust consolidates the surface of the

substrate and is a microbiotope favorable for invertebrates, which populate the space between the crust and the ground. Flowering plants also take part in the pioneer stages of populating the area. Among them, two groups are noticeable. One includes small plants which do not play any essential role in the process of overgrowth: *Juncus biglumis*, *Minuartia rubella*, *Sagina intermedia*, and others. The other group includes species which can form dense stands and, thanks to their powerful root systems, can stabilize the substrate: *Alopecurus alpinus*, *Artemisia tilesii*, *Deschampsia glauca*, *Puccinellia angustata*, and others. In the Arctic, all these species generally prefer bare or weakly turfed, eroded surfaces without a moss cover. The species composition of the pioneer flowering plants is dependent on the regional and latitudinal position and on the character of the substrate. The following species are common in various parts of the tundra zone: *Alopecurus alpinus*, *Luzula confusa*, and *Puccinellia angustata* on landslides in the northern part of the zone; *Arctagrostis arundinacea*, *Cochlearia arctica*, *Deschampsia borealis*, and *Poa alpigena* in the center of the zone; *Dryas punctata* and *Novosieversia glacialis* on fell-fields; and *Artemisia tilesii* and *Festuca cryophila* on loose substrates. Very specific flowering plants are pioneers on the patches in "zonal" communities on "plakor". In the southern tundra subzone, these include *Epilobium davuricum*, *Juncus biglumis*, *Minuartia rubella*, *Pinguicula villosa*, *Sagina intermedia*, and *Tofieldia coccinea*. In the arctic tundra subzone, the first three species are found as well as *Eritrichium villosum*, *Papaver pulvinatum*, *Saxifraga cernua*, *S. nivalis*, *S. platysepala*, *Stellaria edwardsii*, and others. The majority of pioneer species gradually disappear during the formation of the cover and are replaced by others. Nevertheless, the typical peculiarity of the tundra ecosystems is their general taxonomic impoverishment. This is why a number of species remain at more advanced and even terminal stages of succession — for example, *Dryas punctata* on fell-fields and in "zonal" communities in the southern and typical tundra subzones, *Festuca cryophila* on windblown sands and in meadows on southern slopes, *Juncus biglumis* on patches of bare ground and in mires, *Ditrichum flexicaule* on patches of bare ground and in compact moss turf, and *Salix reptans* on river banks in places with ground cryoturbation and in "zonal" communities with closed moss cover.

At more advanced stages with a gradual increase in the thickness of the cover, mosses become the most important part of the ecosystem. They form a compact, relatively loose turf, whose thickness in "zonal" communities on "plakor" can reach 5–8 cm. Dominating species include *Aulacomnium turgidum*, *Hylocomium alaskanum*, and *Tomenthypnum nitens*; other abundant species are *Dicranum congestum*, *D. spadiceum*, *Racomitrium lanuginosum*, and *Rhytidium rugosum*. Liverworts grow in the moss cover, the most abundant and frequent being *Barbilophozia barbata*, *Ptilidium ciliare*, *Sphenolobus minutus*, and *Tritomaria quinquedentata*. All these species create a mosaic. The mosses become a powerful biogenic factor as the compacting of turf proceeds, because they are an important habitat for many organisms, in many respects more favorable than the soil. At the same time, however, they also begin to function as a heat-insulating substrate which in turn reduces the growth of organisms. The negative properties of the moss turf are especially increased when loosely growing species are replaced by species such as *Dicranum elongatum* and *Polytrichum strictum* which form a very compact turf, in which only solitary plants are able to survive. The heat insulation by the moss turf leads in the end to its destruction.

There are various life forms among the tundra plants which are able to live at different successional stages. The mat form, appressed to the surface, is well adapted to arctic conditions. This form is favorable for the survival of plants under the most extreme conditions – for instance, on fell-fields, snowless in winter, subject to winter winds. *Dryas* species show this growth form (*D. ajanensis*, *D. octopetala*, *D. punctata*, *D. schamissonis* and others), as do some other plants, for instance *Saxifraga oppositifolia*. These species establish themselves at early stages of succession, where they are able to exist because of the growth form. In turn, they ensure the existence of different groups of organisms involved in the process of succession. Organic substances are accumulated under the plant mats, and within lifeless rocky areas small "oases" with a good humus layer arise, where a soil population of invertebrates and microorganisms can actively develop. Some other plants will settle in these mats, and thus giving the appearance of fragment of a plant community, relatively far advanced in succession and in contrast to the surrounding areas. The appressed-mat

life form activates the succession process and behaves as an "edificator", changing the environment as a result of the development of an individual.

Perennial taproot plants also influence the environment, among which *Novosieversia glacialis* can be singled out by the strength of its effect. Pockets of peat and then humus are formed under large individuals of this species.

Tussocks of *Eriophorum vaginatum* also represent microcommunities of a specific composition that differ from the surrounding vegetation. These microcommunities are very stable, resistant even to fires, and, after being destroyed as a result of aging, leave behind a large mass of organic material (Polozova, 1970, 1986).

There are groups of organisms which function as pioneers at the initial stages of cover formation, but also complete the succession process at the stage of cover destruction. To these belong some crustaceous lichens and liverworts.

In the process of dynamic changes in the cover, different groups of plants are antagonists towards each other; for example, forbs and grasses in relation to mosses (the former are active and viable in the absence or weak development of the moss cover), and tall shrubs and herbs (under the thick canopy of the former the herb cover is thin). Crustaceous epigeous lichens disappear with the development of mosses. The combination of mosses and dwarf-shrubs can exist with a moderate development of both groups; however, with the increased closing-up of one layer, the other is thinned out. Herbs exert a suppressive influence on the development of dwarf-shrubs, although the latter may survive, though in a suppressed state, under a thick grass cover (for instance, in the meadows on south-facing slopes). The most optimal, and therefore the most stable, combination approaching the climax is a continuous lichen–moss cover (made up of bryoid, mostly pleurocarpous, mosses and fruticose lichens) with a thin layer of dwarf-shrubs, low shrubs, and herbs (sedges and cotton grasses). Such combinations of life forms and groups of plants are best suited to the climatic conditions of the tundra zone and represent the most advanced stage in the succession. This can be observed in the southern and typical tundra subzones. Further north, succession comes to a stop at earlier stages (shrubs are absent in arctic tundra) while neither shrubs nor dwarf-shrubs are found in polar desert).

There are life forms which can exist under the conditions of an arctic climate, but the communities formed prove to be short-lived. One example includes the bog mosses (*Sphagnum*), with their relatively quick upward growth and their ability to form a dense turf, which causes a rise in the permafrost level and a worsening of the hydrothermal regime. Therefore, in the northern part of the tundra zone, the peat-moss hillocks formed by bog mosses are relatively short-lived, unlike the peat bogs of the forest zones which may serve as an example of long-lived self-supporting closed systems. The tall-shrub life form conforms with the climate of the tundra zone only until a closed cover is formed. If shrub thickets close up, the thermal regime in the soil changes unfavorably. As an individual, this life form is compatible with the conditions (although survival is problematic because of the winter winds), but as a type of community it is not. Therefore, tall shrubs are mainly adapted to the depressions of the relief, for example, valleys where the general conditions are less extreme than on the "plakor". On the tundra "plakor", the only tall shrub forming a community is the alder (*Alnaster fruticosus*), although this takes place only in the southern tundra subzone.

The dynamics of the living cover in the Arctic are determined by a strong influence of extreme factors and a weakened response of the living cover. This is due to a low growth intensity, a relatively and absolutely low plant productivity, limitations in the possibilities of establishment in new places, an inhibition of decay, and the predominance of small organisms. Taken together, this results in a situation where the speed of succession is decreased. In the course of their natural development, the tundra ecosystems not only seem but also really are stable. They are unchangeable during the length of time observable by man as compared, for instance, to the forest ecosystems where sharp changes of composition and structure of communities can be observed during one generation of the dominants (e.g., recovery after fires, logging, etc.).

Notions that tundra ecosystems are dynamic are connected not so much with the course and speed of endogenous successions as with the fact that these successions are constantly broken off – that is, endogenous dynamics are weakened, while exogenous dynamics are strengthened. In early stages of succession, the arctic plant cover is a

biogenic factor which improves its own existence and the functioning of the whole ecosystem. At more advanced stages, the cover induces a worsening of the hydrothermal regime in the soil, which slows down and even stops the succession, leading to the destruction of the plant cover and then the entire ecosystem.

Tundra ecosystems exist at the limit of stability with a very slight reserve of endurance. This is why anthropogenic influence so often leads to catastrophic, often irreversible, consequences. Not only may the ecosystems directly subject to man's influence, especially technological influence, be destroyed, but also the whole natural landscape of the area.

One may possibly consider the existence of a single arctic successional sequence which is best realized in the southern tundra subzone and, to a less extent, in the typical tundra where it becomes a relative climax. The sequence of "plakor" communities from the polar desert to the southern tundra subzone may be regarded as analogous to the successional series. The sequence of main groups of plants playing the leading role in the plant cover from the pioneer stage to maturity and from the polar desert down to the forest tundra is: lichens → mosses → herbs → dwarf-shrubs → shrubs → trees. Concurrently, the size of the organisms increases, which is typical of any succession. Under arctic conditions, however, all processes of development are slowed down and, under the most extreme conditions of high latitudes, broken off, often at early stages (for instance, at the herb stage). In polar desert and arctic tundra, it is possible to speak only about the terminal stages of development of the plant cover which have stopped nearer or further from the initial ones (for instance, at the permanent pioneer stages in polar desert and at more advanced stages in arctic and, particularly, in typical tundra). In southern tundra and forest tundra, the elements of the boreal forest succession are superposed on the tundra successional series.

From the viewpoint of successional theory, the problem of climax is especially important in the tundra zone. In the southern and typical tundra subzones, "plakor" communities with a well-developed moss cover, dwarf-shrubs, low shrubs, mesophilous sedges, and lichens show the main features of climax: stability and monotony of structure, high autonomy and environment-forming influence, and relatively low productivity. In the typical tundra subzone, different types of frost-boil tundra with a discontinuous plant cover, but with the same set of life forms and similar species composition, should be considered as "pre-climax". Diversity of species and ecological composition and productivity are greater in these communities than in "zonal" tundras with a continuous cover. The process of the overgrowth of bare-ground patches can be regarded as a model of landscape succession for the tundra in general. There is a tendency to displacement in the maximal values of diversity and productivity to intermediate and even early stages of succession. This is well seen in small soil invertebrates.

In the arctic tundra subzone, "plakor" are occupied by polygonal tundra (bare ground totals more than 50% of the area), which in these more severe climatic conditions is the terminal stage of the spatiotemporal series. They are characterized by the same features as pre-climax (frost-boil) communities in the typical tundra subzone. With a relatively uniform taxonomic composition, a rather variegated set of microgroupings is formed that differ in their quantitative composition. General succession does not reach the terminal climax stage, but stops at the pre-climax. That is in good agreement with the increase in total biomass and diversity of animal populations in spite of the worsening of the climatic conditions.

This tendency is continued in polar deserts, where the plant cover mostly is patchy. In spite of the extreme impoverishment in taxonomic composition, the total soil zoomass is relatively high. Invertebrates attain their optimum in the patchy communities (covering about 20%), analogous to the early and middle stages of overgrown patches of ground in frost-boil tundra. In more closed polar desert communities (cover up to 60%), distinct stages of degradation are observed, which testify to a general incompatibility of such communities with the climatic conditions.

These regularities clearly agree with the general thesis of succession theory, in particular that under extreme conditions successions are cut off at early stages and that maximum diversity and productivity are displaced to pre-climax stages.

SEASONAL DEVELOPMENT

In studies of seasonal development, following the phases of an organism's life cycle, one can see

the main adaptive properties of arctic plants and animals. Most tundra organisms are active only during the snowless and frostless part of the year, but the length of the growing period and the weather conditions, mainly the temperatures of air and soil, vary greatly over the territory of the Far North. On the whole, however, the period of active life in the Arctic is 2–3 months shorter than in the temperate zones of the boreal region. In April and May, when life is awakening in the forest zone, snow still covers the tundra and the temperatures are below 0°C. In September and October, when vegetation is still active in temperate zones, the tundra again subsides into winter dormancy. A polar winter does not only mean snow cover, low temperature, and frozen soil, but also very little light. In this period, therefore, life in almost all groups of organisms comes to a standstill.

In the animal world, about a dozen species of mammals spend winter in an active state: the polar bear (*Ursus maritimus*), the reindeer (*Rangifer tarandus*), the arctic fox (*Alopex lagopus*), the least weasel (*Mustela nivalis*), the ermine (*M. erminea*), the alpine hare (*Lepus timidus*), lemmings (*Dicrostonyx torquatus*, *Lemmus sibiricus*), voles (*Microtus gregalis*, *M. middendorfii*), species of *Sorex*, etc. (Chernov, 1980). In Russia, the great majority of reindeer migrate in winter to the south, outside the tundra limits. Small populations, however, overwinter in some places in the northernmost parts of the tundra zone on the islands Belyi and Novaya Zemlya, on the Novosibirskiye islands, Vrangel island, and in the northern part of Taymyr.

In arctic tundra, where the snow cover is not deep, especially in windblown places, animals are able to obtain plant food in winter. The conditions under the snow cover may be quite favorable for active winter life of lemmings and voles. The rodents make their winter homes in depressions of the relief. They dig numerous passages 10 and more meters from the nest and leave a lot of litter there. The nests are placed only where a constant and sufficiently deep (no less than 50 cm) snow cover settles rather early. Winter is the best period of reproduction for lemmings and determines their numbers. Under-the-snow reproduction has also been recorded for both species of vole. The ermine and the least weasel also have an active life under the snow cover. They hunt for voles and lemmings, using their burrows, passages, and nests. The alpine hare overwinters in the southern part of the tundra, feeding in winter on bush twigs sticking out from under the snow. At the end of winter, when the snow cover is still closed and the temperatures are below 0°C, the polar bear and the arctic fox give birth to their young. Among birds, tundra overwintering is common for the ptarmigan.

The vascular plants of the Arctic may be divided into three groups according to the duration of their leaf system (Serebryakov, 1964; Polozova and Deyeva, 1978). The majority of them are deciduous, losing their leaves at the onset of winter; a very small number are evergreen (with leaves usually living 2–3 years); about one-third of the species are wintergreen or semi-deciduous (the autumn generation or a part of the summer generation of leaves persisting over winter). The plants of the two latter groups have green leaves when snow cover begins in autumn. Some leaves die by the middle of winter, but most species of these groups retain their green leaves until the end of the winter. Slight growth is recorded in April and May, still under the snow (Kovakina, 1952, 1958; Kildyushevskyi, 1956). It is known that some sunlight passes through the snow cover and that the radiation intensity under the snow may be high enough for some carbon dioxide assimilation to take place. A considerable number of species ripen their seeds during the winter. The dominants of tundra vegetation, the mosses, hibernate in a green state.

Thus, a great majority of organisms spend the longest period of the annual cycle in a state of dormancy or a slowing down all life processes. As already mentioned, only a small group of animals overwinters in an active state.

The first migrating birds appear in the tundra at the end of May when the snow cover is still almost closed. Every day brings in more and more new species, and during a two-week period the bird population can become ten times larger. The birds are forced to look for food in places with the least snow cover and on the few thawed patches. The rapidity of the snowmelt and its distribution over the tundra in spring are of great importance to nesting birds. In large birds of prey, like peregrine falcons (*Falco peregrinus*), rough-legged hawks (*Buteo lagopus*), and snow owls (*Nyctea scandiaca*), as well as in waterfowl, such as geese and swans, the period from building a nest to leaving it with the young takes 3.5 months. This is why the birds must begin nesting at the end of May or the beginning of June, since in September they must fly south, and why nesting begins while the snow cover is still almost closed. At this time, there are

still few places for the nests. The well-known cohabitation of "peaceful" birds and birds of prey is sometimes explained by this situation. Close to the nests of the rough-legged hawk, peregrine falcon, and snowy owl, there are often found nests of geese, both *Anser* and *Branta*. Birds of several species are compelled to settle on the first suitable snowless patches. In the early spring, the weather is very unstable, and during recurrent frosts and snowfalls the nestlings of these birds often perish. The first eggs of ptarmigans (*Lagopus* sp.) are laid during the first ten days of June, when the snow-cover is melting, while mass egg-laying in this species begins in the middle of June.

Typical of the very beginning of spring is the awakening of some insect species which appear in masses on the snow surface (Chernov, 1980). It is possible to see dozens of species of springtails, rove beetles (Staphylinidae), and various dipterans, etc. on the spring snow in the tundra. The insects seem to be warmed under the snow by the rays of the sun and make their way to the surface. It is not quite clear how they manage to move through the snow, which is sometimes quite thick. Most probably, they make their way up the plants that are melting out. The main importance of their appearance on the snow surface may be a better use of the heat from the spring sun, thus prolonging the period of active life.

The period of snow thaw is very hard for lemmings. Water floods into their passages and burrows, and there is a great danger of loss of the young which are still in the nests. Lemmings, therefore, migrate in this period from their wintering sites (from mires and ravines with long burrows) to drier places with good drainage, where they make new passages and dig burrows, or renew old ones from earlier years.

Simultaneously with the disappearance of snow is the melting of permafrost. The first parts to thaw out are places without vegetation, especially without a moss cover, such as patches of bare ground in frost-boil tundra, shallows along river banks, south-facing slopes, and tops of hillocks. In the upper thawed layers of soil and moss cover, the soil invertebrates and insect larvae begin their active life after a winter period of rest.

Active growth of mat plants begins after the disappearance of snow when the mean daily temperatures exceed 0°C. Nevertheless, slight growth has been recorded in the subnival areas, the so-called snow "hot-houses" (Aleksandrova, 1961b; Tikhomirov, 1963). These snow "hot-houses" (small cavities between the soil and the snow surface) are formed as a result of the heating of the soil surface or the moss turf by the sun's rays penetrating the snow cover. These "hot-houses" appear when the air temperature is still below 0°C. They are most typical for the arctic tundra subzone where the snow cover is thin. Due to the "hot-house" effect, the plants can start their growth at an air temperature below 0°C. Species overwintering with green leaves acquire anthocyanin coloring, their shoots start growing and their leaf buds start opening. If thawed patches are formed in the places of former snow "hot-houses", then plant development and growth may proceed a little faster, but the course of phenological phases later in the season is little affected.

Plants begin to grow immediately on areas free from snow. The first to start functioning are the leaves of evergreen and semideciduous plants. The anthocyanin coloring changes again to green as chlorophyll is accumulated and carbon dioxide assimilation starts (Gerasimenko et al., 1980, 1988). Shoots start active growth and the leaves begin to develop. The slight growth of these organs in early spring, when the bulk of the roots in the frozen ground are still in a dormant state, is mainly possible because of the dormant reserves in the rhizomes in the upper layers of the soil and in the moss turf, both of which have thawed out by this time. Some plant species may absorb carbon dioxide at ambient temperatures even below 0°C (see, for instance, Tieszen et al., 1980), but the cell temperatures in plant leaves may then be higher. In spite of this, most of the vegetation cover is gray or brown with a slight greenish shade just after snowmelt. However, even less than 10–15 days after the beginning of growth, the first blossoming plants appear (*Draba micropetala*, *Eritrichium villosum*, *Novosieversia glacialis*, *Saxifraga oppositifolia*). In a number of shrub willows, the catkins begin to shed pollen when the branches are still in snow.

The phenological spring in the Arctic lasts about a month or a little less. This is a period of rapid awakening for all groups of organisms. They go through an essential part of the seasonal cycle during a very short period — for example, the birds from arrival to egg laying and the plants from emerging from a state of winter rest to the beginning of general unfolding of leaves and the appearance of the first flowers.

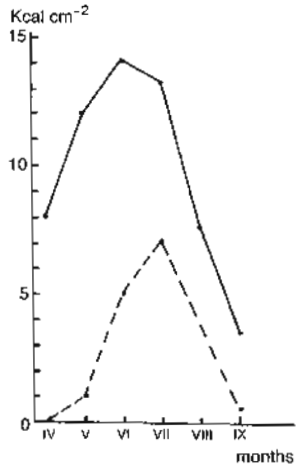


Fig. 16.68. Seasonal changes of total radiation (solid line) and radiation balance (broken line) in Bol'shezemel'skaya Tundra. From Grigor'ev (1956).

In spring, the intensity of biological processes in the Arctic is much higher than in temperate zones. This is connected to a large extent with the light regime in the period. The maximum total radiation in the Arctic occurs in June (Fig. 16.68), at the time of awakening of nature in the tundra. As early as April and May, the amount of solar radiation in the tundra zone is equal to the average monthly amount in the subtropics. This enormous quantity of energy, however, cannot be spent on biological processes since the radiation balance is negative, because of reflection by the snow cover. In June, when the snow cover has melted, the albedo falls sharply, the radiation balance rises, and photosynthesis often proceeds without stop, even during the night.

Summer is the most prolonged part of the vegetation period during which the intensity of life in all its manifestations and in all groups of organisms reaches its maximum. Summer begins in different areas of the polar region during the last days of June or the first days of July. A typical tundra summer starts with an essential rise in temperature (Fig. 16.69). Then usually it continues with cool and rainy weather, after which temperatures may increase even to more than 20°C in July in the arctic tundra. After that, a general lowering of temperature is recorded with sudden changes in August.

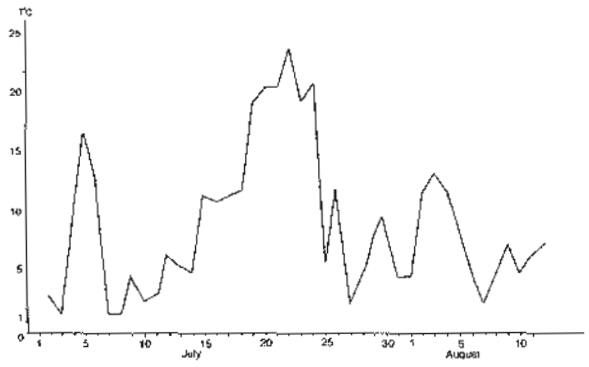


Fig. 16.69. Mean air temperature during the growing season in the arctic-tundra subzone at Dikson, Taymyr, 1979.

In the early works of arctic explorers (Schrenk, 1854; Middendorf, 1869), it was recorded that the short duration of growth leads to the compression of phases of phenological development. An opinion held then was that all arctic plants flowered simultaneously, and mainly constituted a spring flora. However, although blossoming takes place during a compressed period, it still occurs at different times, and it is possible to distinguish seasonal groups among the arctic plant species. This has been supported by observations in all districts of Eurasian tundra and even of polar deserts (Zubkov, 1934, 1935; Shamurin, 1957, 1962, 1966b; Aleksandrova, 1960, 1961a,b, 1963, 1983; Gavrilyuk, 1961; Serebryakov, 1961, 1963; Aleksandrova and Zhadrinskaya, 1963; Moskalenko, 1966; Polozova and Boch, 1970; Malysheva, 1974; Polozova and Deyeva, 1978; Deyeva, 1980).

In spite of the short growing period in the tundra, seasonal differentiation of species can also be observed in various other groups of organisms.

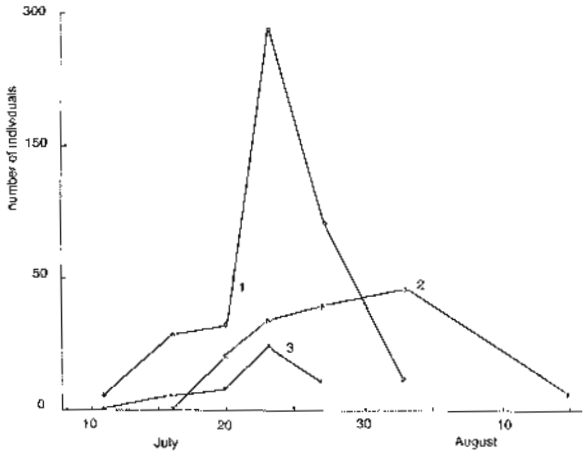


Fig. 16.70. Seasonal changes in numbers of three species of craneflies in the arctic tundra subzone at Dikson, Taymyr, 1979, based on trapping. 1, *Tipula carinifrons*; 2, *T. glaucocinerea*; 3, *T. lionota*. From Lantsov and Chernov (1987).

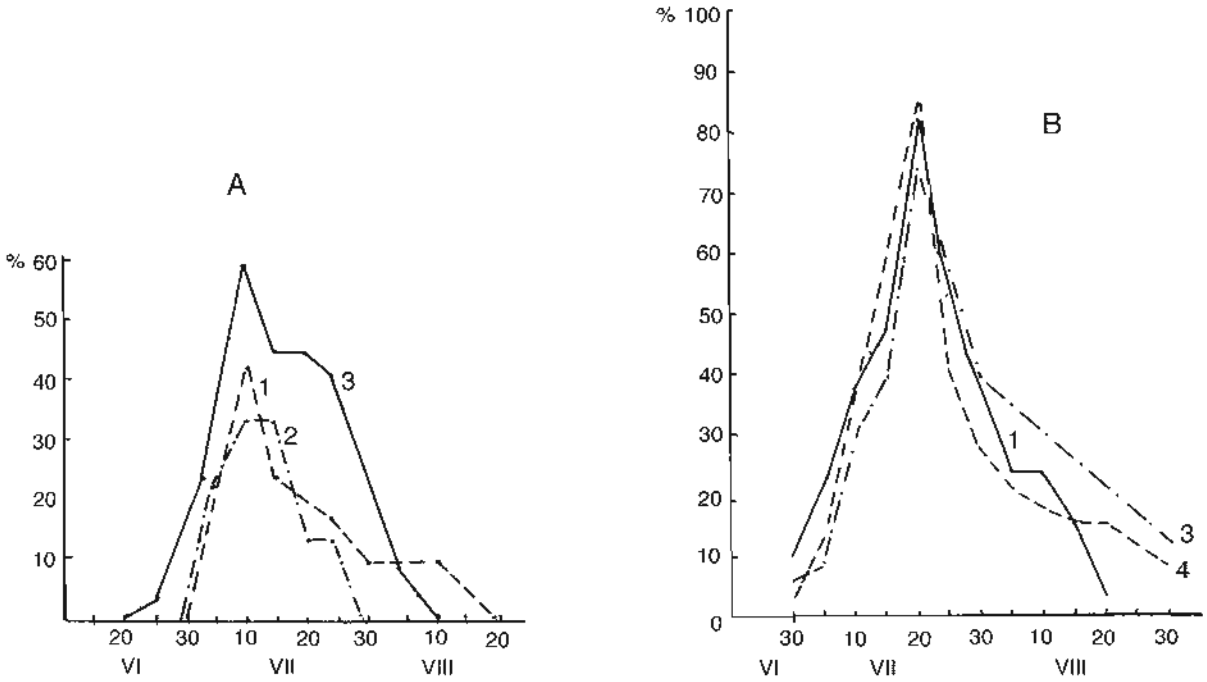


Fig. 16.71. Flowering (%) in different Taymyr plant communities. A, the typical tundra subzone at Tareya in 1967. B, the arctic tundra subzone at Dikson in 1979. 1, in a *Dryas*–sedge–moss hummocky community; 2, in a *Dryas*–sedge–moss frost-boil community; 3, in a herb–grass meadow on a southern slope; 4, in a *Salix polaris*–herb–moss polygonal community. Tareya data from Polozova and Deyeva (1978).

As a rule, the total peak of numbers of different groups of invertebrates and their highest biomass falls in the last ten days of July, although various species give very diverse forms of curves in their seasonal dynamics (see Fig. 16.70).

In the beginning of the phenological summer, more and more new plant species begin to blossom every day. The maximum flowering takes place 20–40 days after snowmelt (generally within the last ten days of July). The blossoming curves of certain plant communities are unimodal (Fig. 16.71) with a fast increase to the maximum and a more gradual descending branch (Polozova and Deyeva, 1978; Deyeva, 1980). The total flowering curve for a region is also unimodal, but with a more gradual slope, especially the descending slope (Fig. 16.72). A large number of species continue to blossom up to the middle of August. The total duration of flowering depends on the meteorological conditions of the year. In colder years, many species increase the period of prefloral growth and budding. In warm years blossoming is more general. Then most species flower simultaneously and the total period of blossoming is shorter. Flowering also depends on the community type (Figs. 16.73, 16.74).

The following plant species flower characteristically at different periods in the Taymyr: Spring: *Draba micropetala*, *Eriophorum vaginatum*, *Eritrichium villosum*, *Novosieversia glacialis*, *Salix arctica*, *S. polaris*, *S. pulchra*, *Saxifraga oppositifolia*, and *Thlaspi cochleariforme*; early summer: *Betula nana*, *Caltha arctica*, *Carex ensifolia* ssp. *arctisibirica*, *Dryas punctata*, *Parrya nudicaulis*, and *Pedicularis oederi*; middle summer: *Arnica iljinii*, *Astragalus subpolaris*, *Carex stans*, *Cerastium maximum*, *Minuartia arctica*, *Myosotis asiatica*, *Polygonum* (*Bistorta*) *viviparum*, *Saxifraga hieracifolia*, *S. hirculus*, *S. nelsoniana*, *S. spinulosa*, and *Stellaria ciliatosepala;* late summer: *Arctophila fulva*, *Artemisia tilesii*, *Comarum palustre*, *Delphinium middendorfii*, *Festuca brachyphylla*, *Koeleria asiatica*, and *Saussurea tilesii*.

The general time and length of flowering is not only characteristic of the various species, but is also affected by variations in the ecological conditions. On south-facing slopes, species begin to blossom 15–20 days earlier than in the communities on "plakor" and mires. In snowbeds melting off by the end of August, flowering appears when most plants in other habitats have already fruited. Species which normally flower in the early polar

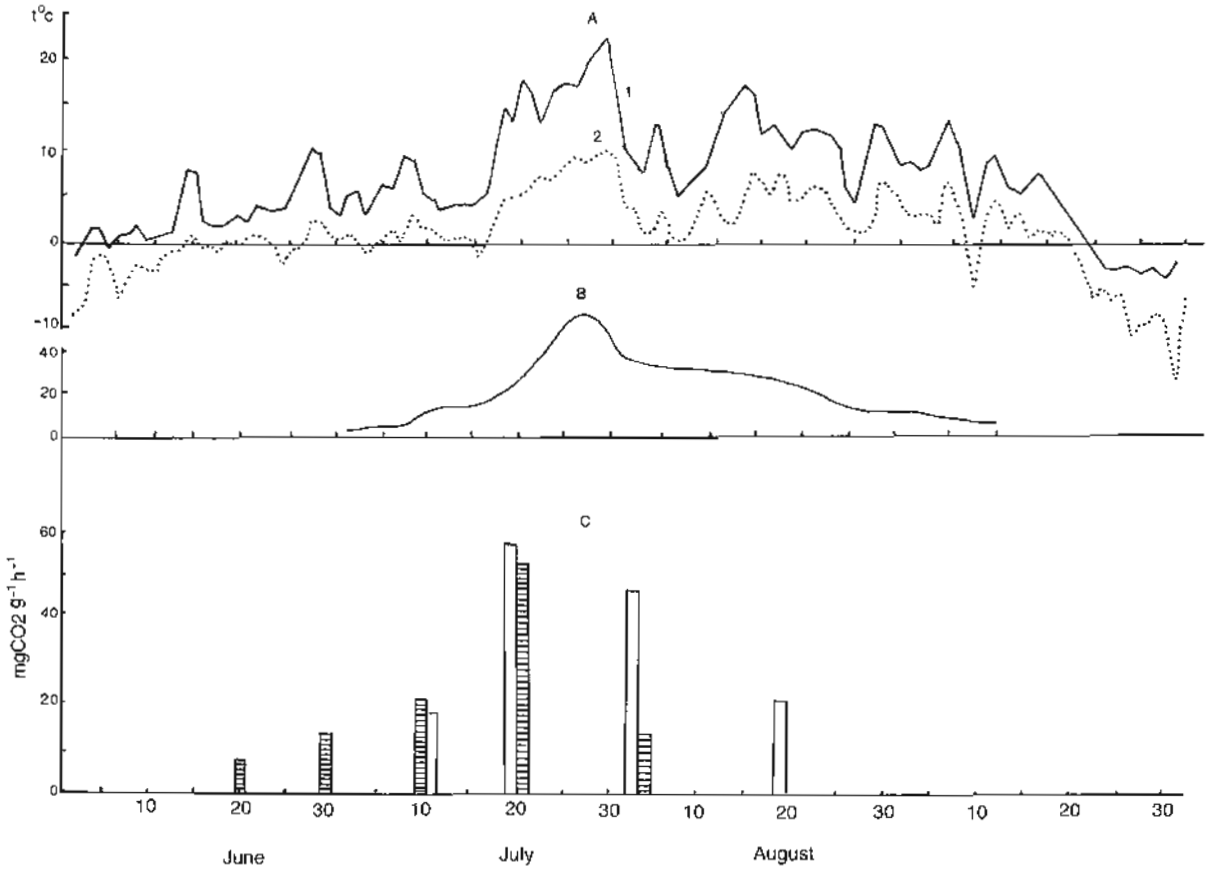


Fig. 16.72. Seasonal course. A, air temperature: maximum (solid line) and minimum (dotted line). B, % of species in flower; C, potential intensity of photosynthesis of main dominant plant in "zonal" communities *Carex ensifolia* ssp. *arctisibirica*; 1, spring generation of leaves; 2, autumn generation of leaves. From Gerasimenko et al. (1980).

spring like *Lloydia serotina*, *Parrya nudicaulis*, *Ranunculus nivalis* and *Salix polaris* may flower in the middle of August when growing in snowbeds. In the arctic tundra subzone, where snow melts very late, blossoming plants can be seen even at the very end of August, shortly before they are hidden by new snow.

The total flowering period depends on the species composition of the communities. In typical tundra, this period is shortest in boggy habitats where the species are generally few and similar in their phenological rhythm. The commonest species here are early-blossoming anemophilous sedges (*Carex chordorrhiza*, *C. stans*, *Eriophorum angustifolium*, *E. medium*), the grass *Hierochloë pauciflora*, and the shrubs *Betula nana* and *Salix reptans* (Polozova and Deyeva, 1978). The longest period of blossoming is observed in meadow communities on south-facing slopes which show the highest species diversity. "Zonal" tundras on "plakor" occupy an intermediate position with regard to the flowering period.

During the period of general blossoming, the color of various types of tundra normally changes with respect to the variety of color aspects formed by abundant species. In "zonal" communities on "plakor", however, the color aspect is only noted during the flowering of the main dominants. In southern and typical tundras in flower, these communities are white due to the flowers of *Cassiope tetragona*, *Dryas punctata*, and *Ledum decumbens*, while in arctic tundras they are yellow because of the blossoming of *Novosieversia glacialis*, *Papaver polare*, *P. pulvinatum*, and *Saxifraga hirculus*. Even in polar deserts, a yellow aspect may be created by poppies in the warmest years. Other dicotyledonous plants are not abundant in "zonal" communities and their blossoming is not so noticeable. The

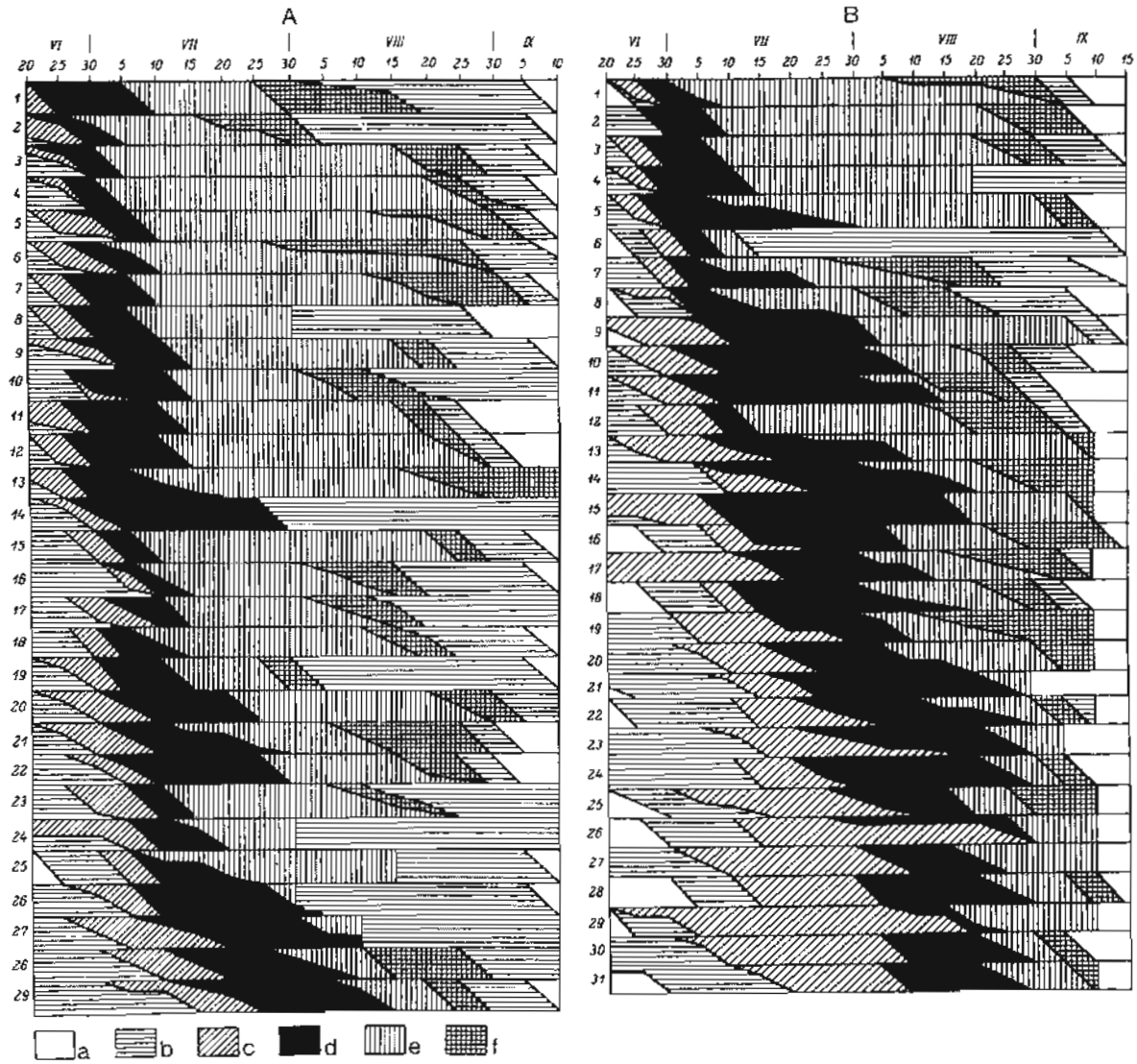


Fig. 16.73. Phenological spectra. A, a "zonal" tundra community on "plakor"; B, a herb–grass meadow on a southern slope in the southern tundra subzone at Kresty, Taymyr. a, dormancy; b, vegetative growth; c, flower budding; d, blossoming; e, ripening of fruits; f, seed shedding. Each line represents one species. A: 1, *Nardosmia frigida*; 2, *Salix pulchra*; 3, *Carex ensifolia* ssp. *arctisibirica*; 4, *Betula nana*; 5, *Arctostaphylos alpina*; 6, *Salix reptans*; 7, *Draba pilosa*; 8, *Pedicularis dasyantha*; 9, *Parrya nudicaulis*; 10, *Dryas punctata*; 11, *Pinguicula villosa*; 12, *Lagotis minor*; 13, *Cassiope tetragona*; 14, *Pedicularis sudetica*; 15, *Vaccinium uliginosum* ssp. *microphyllum*; 16, *Epilobium davuricum*; 17, *Sagina intermedia*; 18, *Luzula nivalis*; 19, *Juncus biglumis*; 20, *Tofieldia coccinea*; 21, *Pedicularis lapponica*; 22, *Pedicularis capitata*; 23, *Minuartia rubella*; 24, *Ledum decumbens*; ; 25, *Saxifraga nelsoniana*; 26, *Andromeda polifolia*; 27, *Saxifraga spinulosa*; 28, *Stellaria ciliatosepala*. 29, *Saxifraga hirculus*. B: 1, *Arctostaphylos alpinus*; 2, *Betula nana*; 3, *Carex melanocarpa*; 4, *Luzula confusa*; 5, *Arabis septentrionalis*; 6, *Salix pulchra*; 7, *Salix nummularia*; 8, *Dryas punctata*; 9, *Polemonium boreale*; 10, *Myosotis asiatica*; 11, *Erigeron eriocephalus*; 12, *Antennaria villifera*; 13, *Astragalus subpolaris*; 14, *Arenaria stenophylla*; 15, *Artemisia borealis*; 16, *Hedysarum arcticum*; 17, *Valeriana capitata*; 18, *Pachypleurum alpinum*; 19, *Cerastium maximum*; 20, *Silene paucifolia*; 21, *Thymus reverdattoanus*; 22, *Astragalus frigidus*, 23, *Dianthus repens*; 24, *Pyrethrum bipinnatum*; 25, *Arnica iljinii*; 26, *Campanula langsdorffiana*; 27, *Koeleria asiatica*; 28, *Sanguisorba officinalis*; 29, *Armeria maritima*; 30, *Poa arctica*; 31, *Arctagrostis arundinacea*. From Zanokha (1986).

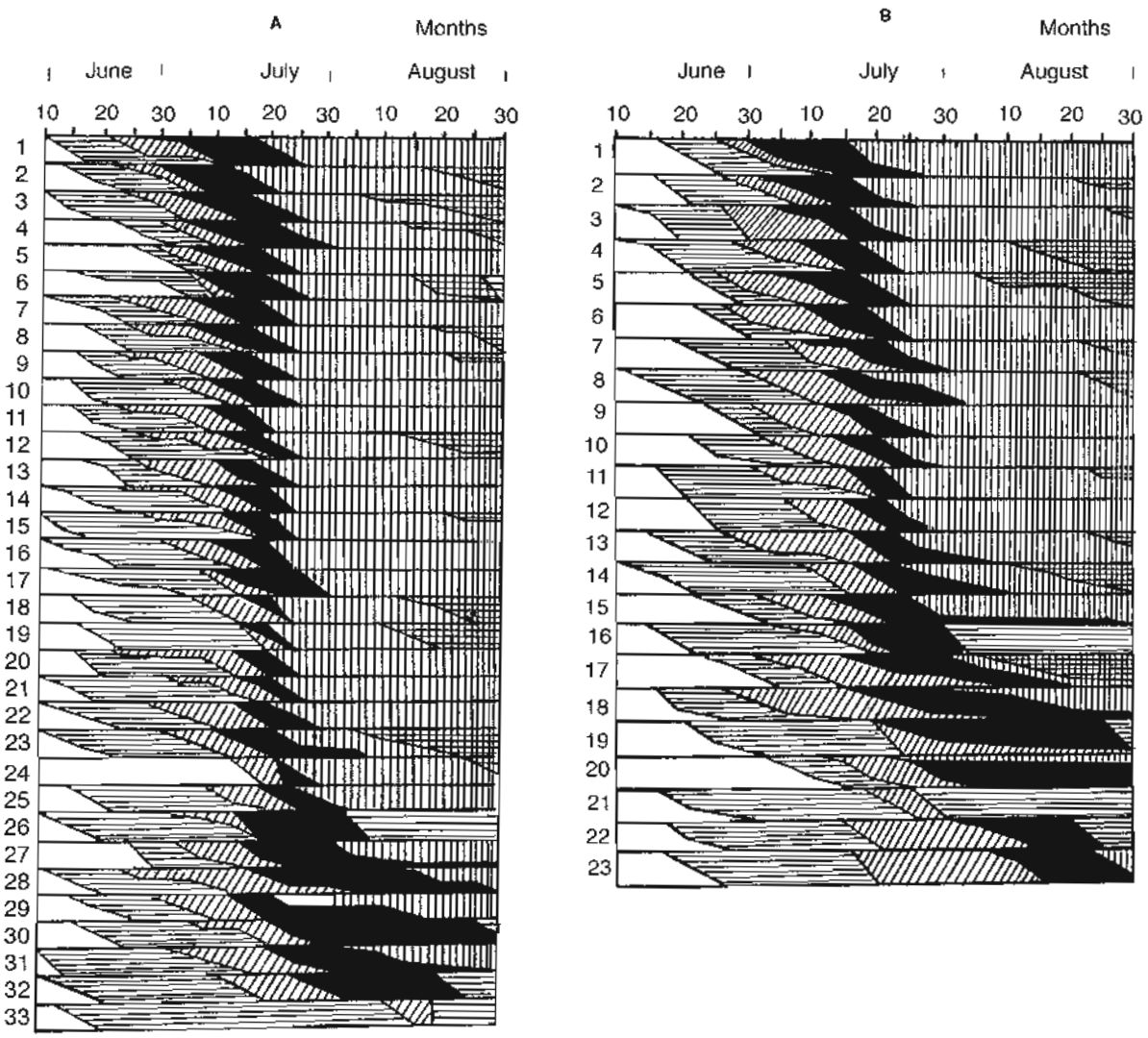


Fig. 16.74. Phenological spectra. A, a "zonal" tundra community on "plakor"; B, a herb–grass meadow on a southern slope in the arctic tundra subzone at Dikson, Taymyr. Shadings as in Figure 16.73. Each line represents one species. A: 1, *Saxifraga oppositifolia*; 2, *Draba subcapitata*; 3, *Salix polaris*; 4, *Eritrichium villosum*; 5, *Parrya nudicaulis*; 6, *Ranunculus sulphureus*; 7, *Pedicularis oederi*; 8, *Cardamine bellidifolia*; 9, *Draba pseudopilosa*; 10, *Saxifraga hieracifolia*; 11, *Saxifraga nivalis*; 12, *Juncus biglumis*; 13, *Luzula confusa*; 14, *Luzula nivalis*; 15, *Eutrema edwardsii*; 16, *Carex ensifolia* ssp. *arctisibirica*; 17, *Dryas punctata*; 18, *Minuartia rubella*; 19, *Sagina intermedia*, 20. *Saxifraga nelsoniana*; 21, *Saxifraga platysepala*; 22, *Saxifraga caespitosa*; 23, *Cerastium beeringianum* ssp. *bialynickii*; 24, *Gastrolychnis apetala*; 25, *Minuartia macrocarpa*; 26, *Alopecurus alpinus*; 27, *Pedicularis sudetica*; 28, *Saxifraga hirculus*; 29, *Papaver polare*; 30, *Stellaria crassipes*; 31, *Saxifraga spinulosa*; 32, *Deschampsia borealis*; 33, *Arctagrostis latifolia*. B: 1, *Saxifraga oppositifolia*; 2, *Draba subcapitata*; 3, *Draba glacialis*; 4, *Salix polaris*; 5, *Pedicularis oederi*; 6, *Lloydia serotina*; 7, *Cochlearia arctica*; 8, *Papaver polare*; 9, *Eutrema edwardsii*; 10, *Dryas punctata*; 11, *Draba pseudopilosa*; 12, *Saxifraga nivalis*; 13, *Saxifraga caespitosa*; 14, *Cerastium beeringianum* ssp. *bialynickii*; 15. *Myosotis asiatica*; 16, *Alopecurus alpinus*; 17, *Taraxacum arcticum*; 18, *Saxifraga hirculus*; 19, *Stellaria ciliatosepala*: 20, *Saxifraga cernua*; 21, *Poa alpigena*; 22, *Festuca cryophila*; 23, *Deschampsia borealis*.

main color aspect in "zonal" communities falls within the first ten days of July and lasts about a week. The generally later blossoming of grasses, sedges, and willows, the most widespread plants, does not distort the general green coloring of the plant cover because of the less colorful flowers.

A different picture can be seen on the meadows on southern slopes, where, for instance, as many as 5–7 color aspects give place to one another in the typical tundra subzone during more than a month: white-rose (*Lloydia serotina*, *Parrya nudicaulis*), yellow (*Astragalus umbellatus*, *Pedicularis oederi*),

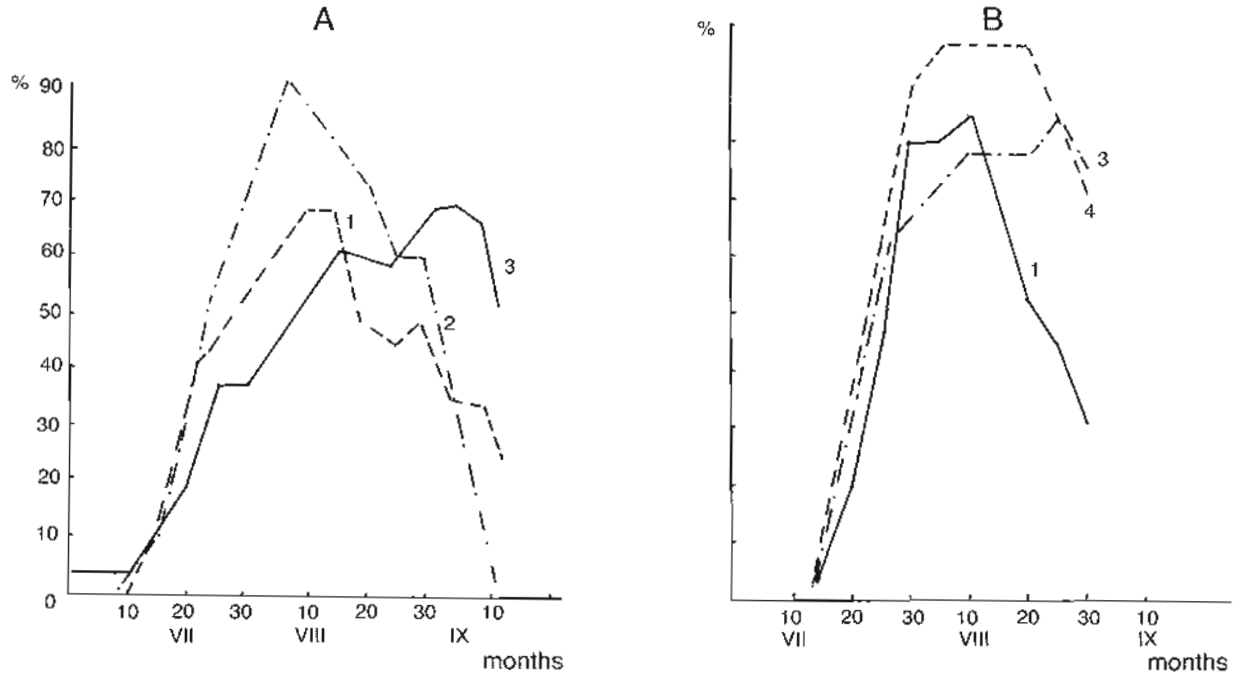


Fig. 16.75. Fruiting curves. Designations as in Figure 16.71.

crimson (*Astragalus subpolaris*, *Hedysarum arcticum*, *Pedicularis verticillata*), white (*Cerastium maximum*, *Polygonum bistorta* (*Bistorta major*), *P.* (*Bistorta*) *viviparum*, *Valeriana capitata*), and orange-yellow (*Arnica iljinii*, *Senecio resedifolius*, *Taraxacum ceratophorum*.

In wet habitats, there are very few dicotyledons with bright flowers (*Caltha arctica*, *Cardamine pratensis*). During the general flowering peak period in other tundra habitats, a white aspect here is produced by fruit-bearing *Eriophorum angustifolium* and *E. scheuchzeri*.

The peak of flowering, both in terms of the number of species and of individual plants, falls as mentioned within the last ten days of July and marks the maximum of the tundra summer. This is the time of the highest stable air temperatures and of cloudless fine days in the continental part of the tundra zone. The soil has then melted throughout the whole depth of the seasonal active layer and is maximally warmed up.

By the beginning of the mass flowering of tundra plants, the early spring species have already started fruiting. The maximum number of species in the fruit-bearing phase, however, has been recorded at the end of July and the beginning of August in years of good or moderate weather conditions (Polozova and Deyeva, 1978; Deyeva, 1980) and at the end of August during cold years. The curves for fruiting are unimodal (Fig. 16.75), like those for flowering.

The height of summer is not only the most important phase of phenological development, which in many ways is responsible for the success of the whole generative cycle. It is also the time of highest photosynthetic intensity, of maximum linear growth of leaves and shoots, and of maximum aboveground productivity of vascular plants.

Seasonal differences are also observed in the vegetative organs of plants. The linear growth of leaves and stems takes place mainly from the beginning of July to the beginning of August (Pospelova, 1972; Vital, 1978, 1980). Plants may be divided into three groups according to the timing of their growth in relation to flowering (Polozova and Deyeva, 1978). The first group includes plants completing their growth before the beginning of blossoming. These are mainly late-flowering plants like *Delphinium middendorfii*, *Hedysarum arcticum*, *Ledum decumbens*, *Orthilia obtusata*, *Pedicularis capitata*, *Potentilla stipularis*, *Pyrola grandiflora*, *Saussurea tilesii*, *Senecio atropurpureus*, and *Vaccinium vitis-idaea*. The second group completes growth after flowering. This group includes the early blossoming plants *Betula nana*, *Draba hirta*, *D. micropetala*, *D. oblongata*, *Dryas punctata*, *Eu-*

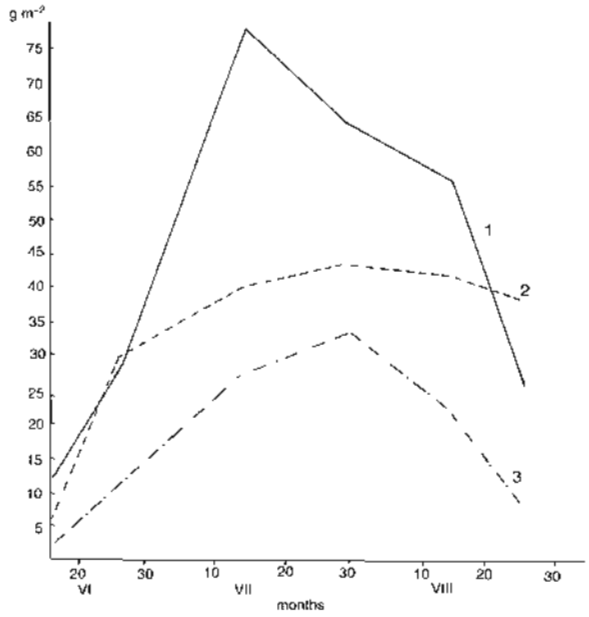


Fig. 16.76. Seasonal dynamics of green parts of herbs in a herb-grass meadow on a southern slope in the typical tundra subzone by the Rogozinka River, Taymyr, 1983. 1, grasses; 2, legumes; 3, other forbs.

trema edwardsii, *Pedicularis dasyantha*, *P. oederi*, *Salix pulchra*, *S. reptans*, *Saxifraga oppositifolia*, and *Thlaspi cochleariforme*. The third plant group completes growth simultaneously with blossoming in the middle of summer and includes *Carex ensifolia* ssp. *arctisibirica*, *Cassiope tetragona*, *Lagotis minor*, *Oxytropis middendorfii*, *Rubus chamaemorus*, *Saxifraga spinulosa*, and *Valeriana capitata*. In a great majority of plant species, the maximum growth in length (up to 6–10 mm day^{-1}) is recorded before blossoming and is reduced again by the end of July.

Productivity of aboveground organs of vascular plants reaches its maximum by the beginning of August, after which it decreases (Fig. 16.76).

A well-pronounced seasonal course of the photosynthesis rate is also observable. Most plants begin to absorb carbon dioxide at temperatures about 0°C (Shvetsova and Voznesensky, 1970; Gerasimenko and Zalenskyi, 1973; Gerasimenko et al., 1980). In the late spring period, simultaneously with the beginning of leaf and shoot growth, there is a marked rise in photosynthesis rate. Most photosynthesis in semideciduous plants is performed by over-wintering leaves. During early summer, active growth of new leaves takes place concurrently with the dying of the previous year's leaves.

In the main group of deciduous plants, leaves are formed early. The maximum rates of photosynthesis are recorded around the middle of July (Fig. 16.72). At the same time, growth processes and weight increase reach their peak. The maximum potential intensity of photosynthesis coincides with the time when the majority of plants are coming into flower (Fig. 16.71), while for species with rapid seasonal development (which complete the growth of their leaves and shoots after blossoming) it coincides with the onset of fruiting. On the whole, the largest values of potential photosynthe-

TABLE 16.23

Frequency of visits of flowers by bumblebees in the typical tundra subzone at Tareya (Taymyr) in 1969[1]

Plant species	June	July			August
	21–30	1–10	11–20	21–31	1–10
Oxytropis nigrescens	+++	+	–	–	–
Pedicularis dasyantha	++	+	–	–	–
P. oederi	+++	+++	++	+	–
P. sudetica	++	++	++	–	–
P. verticillata	+	++	+++	++	++
Oxytropis middendorfii	–	++	+++	+	–
Astragalus subpolaris	–	+	+++	+++	+++
Oxytropis adamsiana	–	–	+	+++	++
Astragalus umbellatus	–	–	+	+++	+
Hedysarum arcticum	–	–	+	++	++
Delphinium middendorfii	–	–	–	++	++

[1] From Chernov (1978a).
+, rare; ++, common; +++, very common.

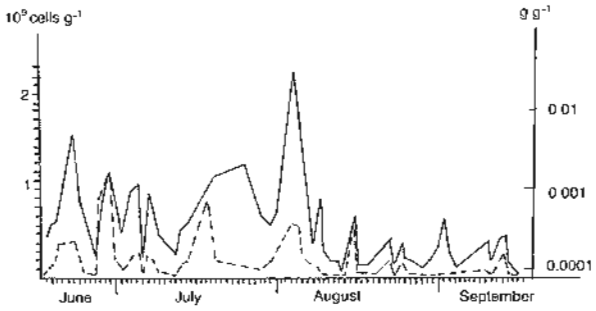


Fig. 16.77. Numbers (solid line) and biomass (broken line) of bacteria per gram of oven-dry soil in a *Betula nana–Carex ensifolia* ssp. *arctisibirica*-moss frost-boil community in the southern tundra subzone at Kresty, Taymyr through the period 18 June–15 September 1976. From Parinkina (1986).

sis coincide with the highest rate of growth. In late summer, as a result of the decrease in radiation, reduction in day length, a general fall of temperature, sometimes even with the after-effects of night frosts, and the ageing of the leaf apparatus, the rate of photosynthesis sharply decreases. Changes in the makeup of the flowering population during the growing season greatly affect the food relations of the dependent fauna (Table 16.23). Differences in the time of blossoming is one way in which plants adapt to coexistence in the community. For insect-dependent plants (entomophils), this is of a great importance because there is an obvious lack of effective pollinators in the Arctic. Among the entomophilous species, a kind of competition for pollinators is possible (Chernov, 1978a).

The most difficult period for insects is the end of June, when the weather conditions are already favorable for insect flight, especially for bumblebees, but few plants are flowering. The feeding spectrum of insects is particularly varied in mid and late July. The majority of specialized entomophilous plants are concentrated in meadow communities which occupy small areas. This makes the possibility of pollination easier even when many species are flowering simultaneously. It is, as already mentioned, typical that in meadows the flowering period is most prolonged, the number of color aspects is the greatest, and the time of flowering of various groups of plants differs most. All this, undoubtedly, aids in successful pollination.

Two main maxima can be recorded during the vegetation period in the development of microflora (Fig. 16.77) – namely, early in spring and at the end of the phenological summer (the end of July–beginning of August). The spring peak is due to the rise in air and soil temperature, melting of snow, and input into the soil of available nutrients extracted from litter as well as from lemming excrement. The second maximum is connected to the input of root secretions, of above- and belowground dry matter, and of the products of activity of meso- and microfauna. A general decrease in the microflora starts in the second part of August, with a sharp reduction in September. Seasonal dynamics are less variable in the saturated biotopes and more pronounced in "zonal" communities on "plakor". Microbiologists (Parinkina, 1989) record a peculiar sequence of seasonal dynamics of microbial populations in tundra soils, with sharp but very short increases and decreases in numbers of cells (Fig. 16.78). The amplitude of these variations is very large in the typical tundras, less in the arctic tundras, and minimal in the polar deserts where the density of microbial populations is extremely low.

During the first ten days of July (at the beginning of mass flowering) the first bird eggs are hatched. From the middle of July, and especially at the end of the month, the young of many species are hatched. At the end of July down-covered

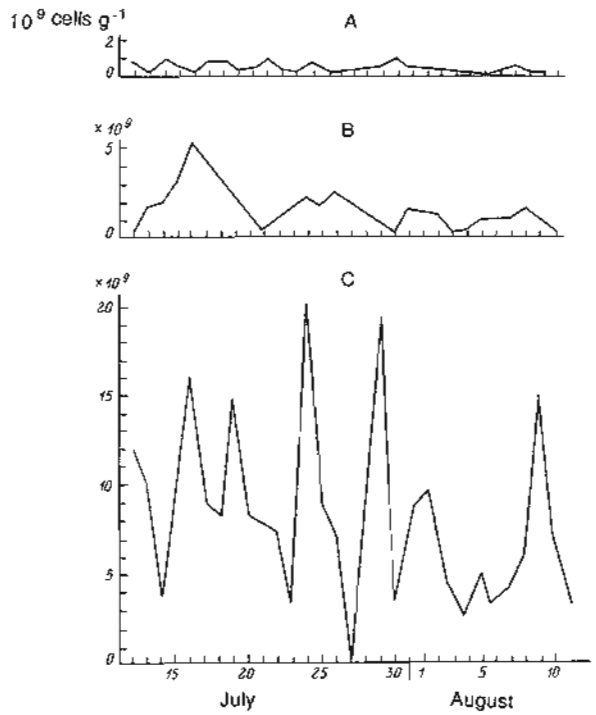


Fig. 16.78. Seasonal changes in numbers of bacteria. A, polar desert; B, arctic tundra; C, typical tundra. From Parinkina (1989).

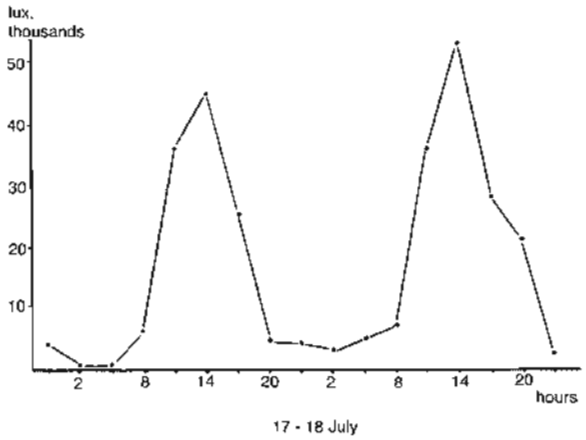


Fig. 16.79. Diurnal changes in light intensity (10^3 lux) in the arctic tundra subzone at the mouth of the Uboinaya River, July 17–18, 1988.

nestlings are common. At the beginning of August, many young birds start flying and in the middle of August they begin to form flocks.

The summer in the Arctic has one peculiarity which sharply distinguishes it from that of temperate zones, namely the 24-h solar radiation. This enables the plants to absorb carbon dioxide day and night and makes it possible for pollinating insects, birds, and reindeer to feed throughout the 24-h period. In other words, the period of activity of many groups of organisms is increased.

The radiation intensity at the peak of the summer in July changes considerably more during a 24-h period than in June. The maximum radiation, about 50,000–100,000 lux, is observed at midday. At night, radiation in July is reduced to one-tenth, with a maximum of 5,000–10,000 lux (Fig. 16.79).

The rhythm of diurnal radiation is reflected in the behavior of pollinating insects (Chernov, 1978a). The daily dynamics of activity of the majority of tundra anthophils is rather strictly unimodal (Fig. 16.80). In many species, the time of maximum activity in the tundra is shifted more towards the afternoon hours than in more south-

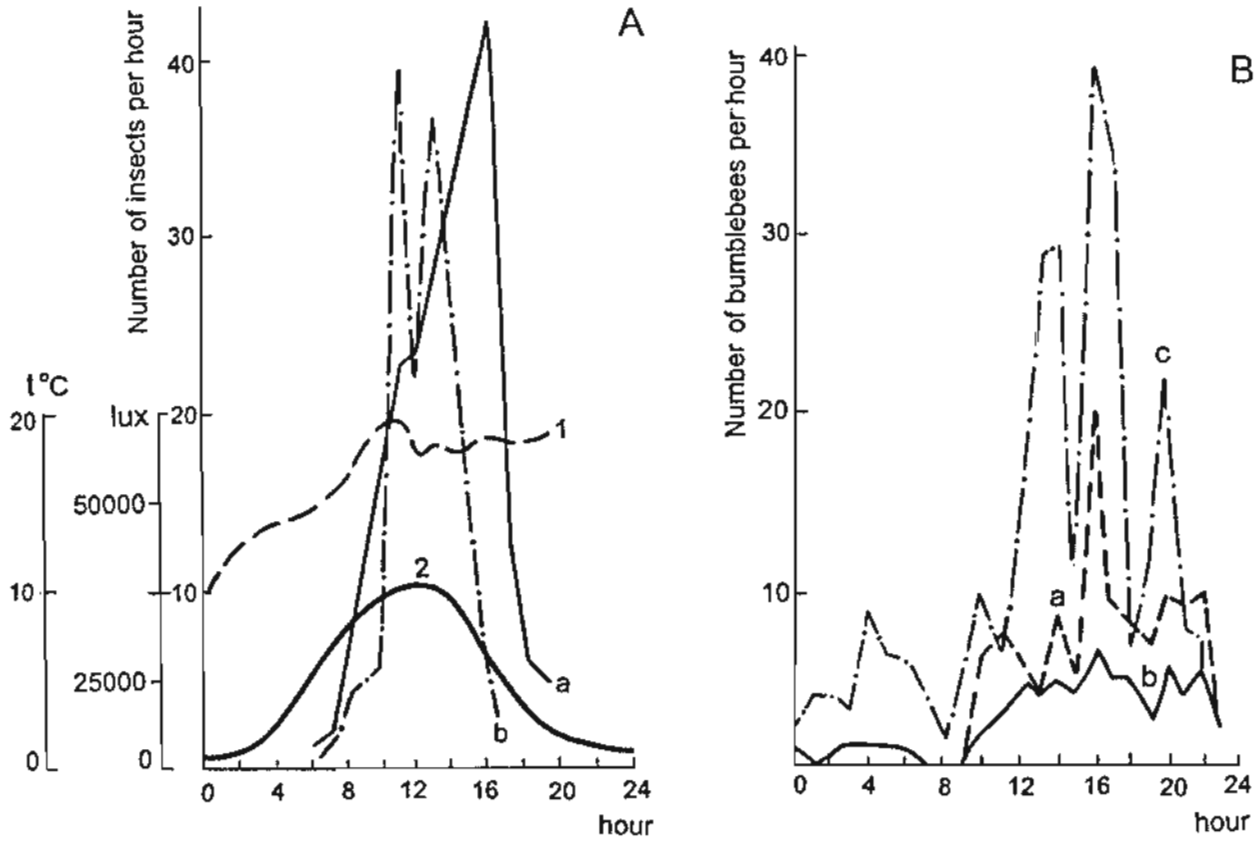


Fig 16.80. Diurnal changes in light intensity, air temperature, and active flight of some insects in the typical tundra subzone at Tareya, Taymyr, July 1969. A: a, number of flies of the genus *Helophilus*; b, number of butterflies of the genus *Colias*; 1, air temperature; 2, light intensity. B: diurnal activity of bumblebees. a, total bumblebees visiting the flowers recorded in the sample plot; b, bumblebees visiting the flowers of *Astragalus subpolaris*; c, bumblebees flying over the sample plots. From Chernov (1978a).

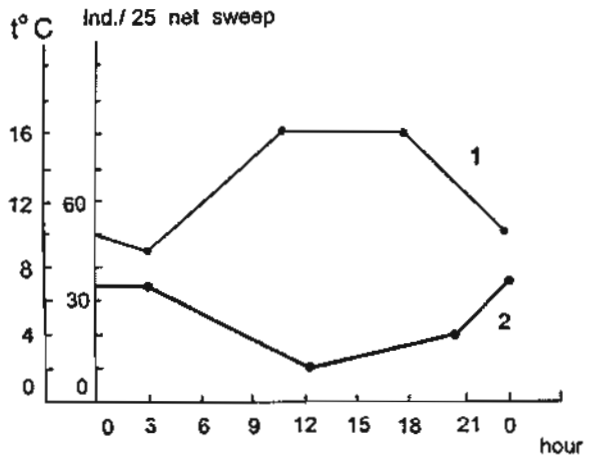


Fig. 16.81. Sawfly larvae in herb–grass meadow on a south-facing slope. Tareya, Taymyr, August 2–3, 1966. 1, air temperature; 2, sawfly larvae caught in upper part of herb layer per net sweep.

erly regions. As a rule, their activity falls after 20:00–21:00 h and rises again about 07:00–09:00 h. This course of activity takes place only while temperatures are sufficiently high in fine weather. Even on the warmest days with maximum temperatures of + 10–20°C, the period of high activity of bumblebees may start as late as 10:00–11:00 h, but may, on the other hand, last till 21:00–22:00 h. During fine weather, some bumblebees fly even at night. Unstable weather, so typical for the tundra summer, causes considerable changes in the diurnal course of insect activity. There are days when anthophilous insects do not fly at all, but if the weather improves during the night, they may even then begin to visit flowers.

At the peak of the polar summer in July, the diurnal rhythm is also characteristic of the inhabitants of the herb layer. As in more southerly biomes, many insects move to the upper part of the vegetation at night when they feed intensively and return to the lower parts of the vegetation at midday when the air temperature is maximal. Such behavior is very typical, for instance, of butterfly caterpillars and sawfly larvae (false caterpillars) (Fig. 16.81). This can probably be explained by a change in humidity, to which they are very sensitive.

Daily dynamics are also noticeable in the intensity of photosynthesis. Due to differences in radiation during daytime and nighttime hours, net photosynthesis even in June may be positive during less than 24 hours. In many species net photosynthesis does not occur between 22:00 and 04:00 h, or is then very close to the compensation point. In some species carbon dioxide may even be released during the night at about 3 mg CO_2 g^{-1} h^{-1} (Gerasimenko and Shvetsova, 1988). Net photosynthesis may also cease during daylight hours in the case of heavy cloud cover, when there are sharp falls in temperature, or during drought (Kjelvik et al., 1975). In spite of this, the average daily duration of visible photosynthesis (16–20 h) in plants in the Arctic is longer than in temperate zones. This means that in the Arctic the diurnal plant production in early summer may be of the same order as in temperate regions. The highest photosynthetic rates have been recorded in the afternoon hours when the daily maxima of radiation and temperature are observed (Fig. 16.82). The curves of the diurnal course in intensity of potential and net photosynthesis differ depending on weather conditions (cloudiness and air temperature). On sunny cloudless days, the curves are normally single-peaked or dome-shaped; on cloudy days with massive cloud cover they are smoother because of smaller differences between day and night. On days with sharply changing cloudiness they may have one, two, or many peaks with considerable drops in between. Sharp rises in the rate of carbon dioxide absorption coincide with the strongest increase in radiation during the 24-h period. On some hot sunny days, the diurnal maximum of potential net photosynthesis occurs in the morning hours instead of midday, when, due to the overheating of leaves and closing of stomata, the intensity of photosynthesis falls (the air temperature close to the leaves reaches 28–30°C, while the leaves themselves are heated to 32–35°C). At the beginning and the end of the growing season, the daily duration of net photosynthesis is lowered because of the shortening of the day (Shvetsova and Voznesenskyi, 1970; Gerasimenko and Zalensky, 1973; Gerasimenko et al., 1980, 1989).

All things considered, most of the seasonal plant productivity is normally performed during the daytime hours. At the beginning of the growing season when radiation at night is high enough, the night productivity of photosynthesis may reach 10–20% of that during the day. However, at the end of summer when radiation decreases and there is often also a heavy cloud cover, a decrease in organic matter is observed at night, as shown by the release of carbon dioxide. Unstable weather of

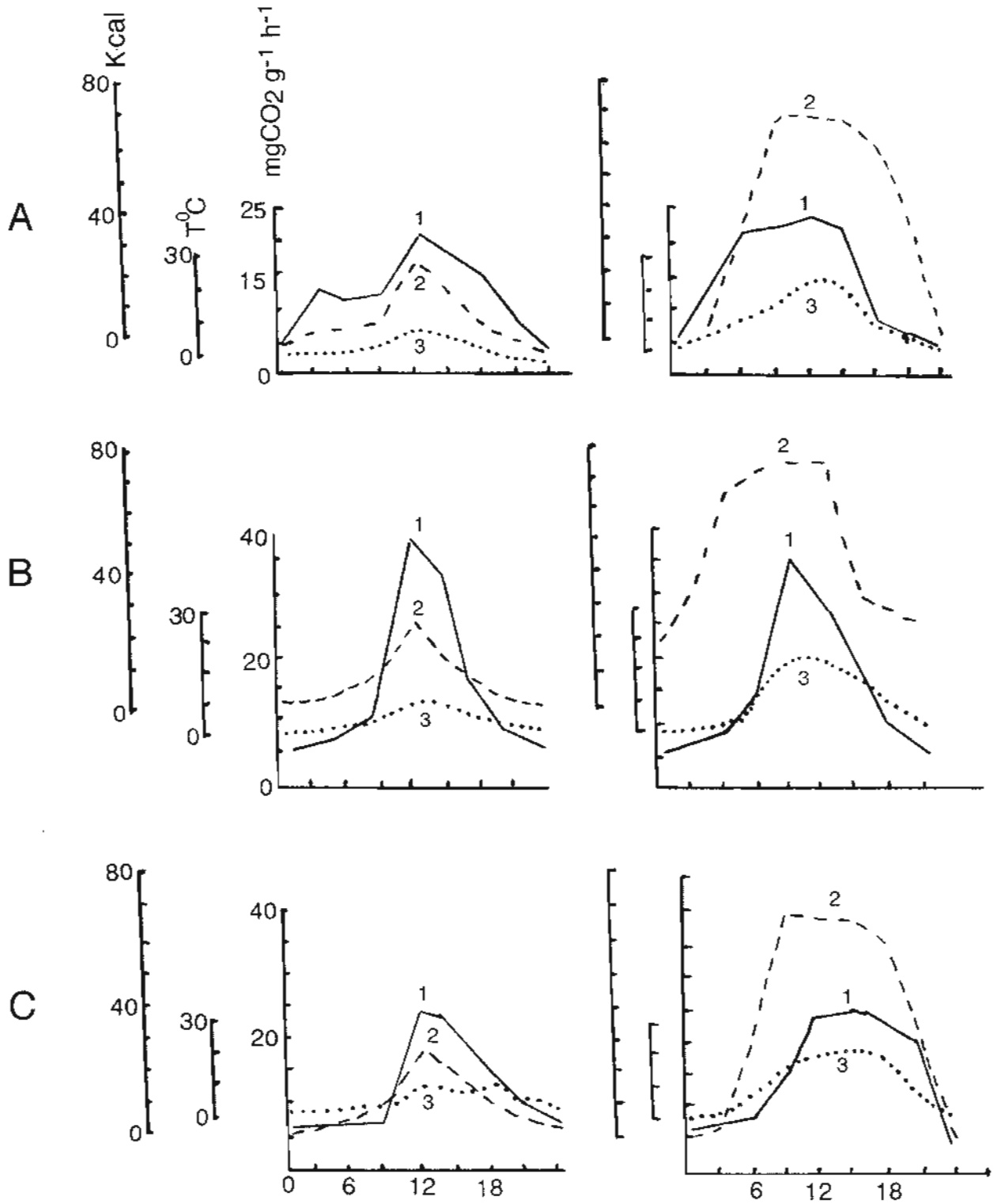


Fig. 16.82. Diurnal variations in (1) potential intensity of photosynthesis, (2) light intensity, and (3) leaf temperature in a growth chamber in the typical tundra subzone at Tareya, Taymyr, 1972. A, *Vaccinium vitis-idaea* ssp. *minus*; B, *Pyrola grandiflora*; C, *Rubus chamaemorus*. Left at low light intensity and right at higher light intensity. From Gerasimenko et al (1980).

the tundra zone, dense low-level cloud which decreases radiation by a factor of 2–10, rain, possible frost, snowfall, etc. may reduce both the intensity and the time of net photosynthesis. Unfavorable weather conditions prevent plants from fully using their potentialities for more productive assimilation.

The most important adaptive property aiding cross-pollination is the diurnal rhythm of blossoming. In the temperate zone with a clearly pronounced change of day and night, synchronization of the rhythm of flowering, as a special case of the circadian rhythm of physiological processes, is quite natural. In the Arctic, a total absence or only a slight manifestation of a diurnal variation in blossoming might be expected, but this does not seem to be fully true (Tikhmenev and Levkovskyi, 1973; Shamurin et al., 1974; Tikhmenev, 1976). A diurnal flowering rhythm is quite pronounced in a comparatively small number of species. This is observed in some species which open and close their flowers or inflorescences at fixed times of the day for several days in succession. These include some species of Asteraceae (*Crepis, Taraxacum*), Caryophyllaceae (*Gastrolychnis, Silene*), and Gentianaceae (*Gentiana algida*). Other species have flowers which are open at a strictly determined time of the day. Blossoming mainly during the morning hours are *Alopecurus alpinus*, *Claytonia arctica*, *Hierochloë alpina*, *Papaver polare* and *Potentilla nivea*, while others open their flowers in the evening – for instance, *Festuca haffinensis* and *F. brachyphylla*.

The fluctuation of radiation intensity during the summer in the Arctic is sufficient for the daily rhythm of blossoming to be established in these species. It is typical that most of these species flower in the second half of July when differences in radiation between day and night hours have already become well pronounced. For the majority of species with flowers opening only once, especially among entomophils, however, they are usually open during a considerable part of the 24-h period and sometimes continuously. The peak of flower unfolding is normally during the warmest hours around noon, but at times of sudden rises of temperature this may be shifted towards the afternoon and even nighttime hours. This shows that temperature change may also affect the flowering rhythms. Both in June and in July, the differences between the day and the night temperatures reach 5–10°C. Thus, although the 24-h illumination in the first half of the polar summer contributes to a certain degree to the increase in duration of some biological processes and thereby intensifies the functioning of the polar ecosystems, there are clear decreases in the intensity of physiological and ecological processes in the nighttime hours.

The most typical features of a polar summer are the recurrence of frost and summer snowfalls. In the southern tundra, these are rather seldom, in typical tundra almost every year, though not very often. In the arctic tundra and in polar desert in unfavorable years, snow may fall during the entire summer (Aleksandrova, 1961b). Usually such snow remains on the ground for less than 24 hours, but sometimes it will stay for 2–3 days. The air temperature falls sharply and becomes negative. Summer snowfalls are harmful to flowers, nesting birds, and some insects, especially to the bumblebees which have begun to feed their progeny. But, on the whole, the tundra plants and animals are adapted to this phenomenon and endure summer snowfalls without great losses. Only a few individuals are damaged or perish.

The phenological summer in the tundra is completed by the middle of August. Its general duration is about 1.5 months. It lasts from the active unfolding of leaves and shoot growth through flowering and shows a very active faunal life until the time when the majority of plant species change to the phase of fruiting and the birds begin to form flocks for departure.

Autumn is the shortest part of the growing season. According to the calendar it begins in the middle of August. Nevertheless, the first signs of autumn may be recorded as early as the beginning of August. In some plants, the leaf colors then begin to change. This is partly connected with night frosts, but no less important is the change in the character of radiation. In August, total radiation falls sharply and the radiation balance decreases. Already at the beginning of August (in Taymyr on August 1–2 in southern regions and on August 7–8 in the more northerly typical tundra), the sun begins to go below the horizon and the 24-h polar day comes to an end. In western Taymyr the meteorological conditions of August 1982 were not worse than in July because of an abnormally long period of southerly winds. There were no night frosts in August that year and the average daily air temperature was about 10°C during almost the entire month. In spite of this, reddening of leaves was, as usual, observed in the first ten days of August.

The second half of August is the time of fruit ripening. The tundra plants are divided into groups with very slow-ripening (ripening of seeds 50–75 days), slow-ripening (40–50 days), medium slow-ripening (35–40 days) and fast-ripening (less than 30 days) plants (Gavrilyuk, 1961). Heath-like dwarf-shrubs belong to the first group. For example, in *Cassiope tetragona*, this period occupies 70% of the entire growing season. A long fruiting period is generally observed in plants with juicy fruits (*Arctostaphylos alpina*, *Rubus chamaemorus*, *Vaccinium uliginosum*, *V. vitis-idaea*). This is probably why they do not grow far to the north, and why some of them, although they grow in the typical and arctic tundra subzones, do not bear fruit there. The most quickly ripening fruits are most often small and dry and belong to representatives of the families Asteraceae, Caryophyllaceae, Portulacaceae, and some Brassicaceae such as *Cochlearia* and *Draba*. Within a district, the fruiting period varies in a species with regard to the beginning of growth and the meteorological conditions. Thus, in *Cassiope tetragona* it can occupy 50–70 days and in *Empetrum hermaphroditum* 50–60 days. Differences in the duration of fruiting lead to different probabilities of ripening by the end of the growing season. According to the regularity of fruit ripening, plants of the tundra zone may be divided into three groups (Deyeva, 1980). Species with regular, almost annual ripening (except for abnormally cold years) are *Chrysosplenium alternifolium*, *Dryas punctata*, *Eriophorum angustifolium*, *E. vaginatum*, *Juncus biglumis*, *Pedicularis oederi*, *P. verticillata*, *Ranunculus borealis*, *Salix arctica*, *S. lanata*, *S. polaris*, and *S. pulchra*. Species with a medium regularity of ripening (seeding in warm and moderate years) are *Betula nana*, *Carex ensifolia* ssp. *arctisibirica*, *Oxytropis middendorfii*, *Pachypleurum alpinum*, and *Polemonium boreale*. Species with extremely irregular ripening of fruits (they ripen and seed only in the warmest years) are *Arctagrostis latifolia*, *Arctophila fulva*, *Artemisia tilesii*, *Astragalus subpolaris*, *Dupontia fisheri*, *Poa arctica*, and *Valeriana capitata*.

The most widespread plants, dominants of the "zonal" communities, belong to the second group. However, every year some plants (sometimes few, sometimes many) are snowed under, carrying seeds which are to some extent immature (Khodachek, 1970, 1978; Deyeva, 1980).

In some species, the generative cycle becomes incomplete as one moves north. For example, bog bilberry (*Vaccinium uliginosum*) in forest tundra bears fruit abundantly and its berries ripen every year. In southern tundra, this species fruits only in some years, and usually poorly. In typical tundra the species flowers, but bears no fruits; while in arctic tundra it is always in a vegetative state. The cloudberry (*Rubus chamaemorus*), which is mass-fruiting in the forest tundra and southern tundra, does not bear fruit regularly in the typical tundra. This phenomenon is observed only in boreal and hypoarctic species. In arctic and arctic–alpine species, including dominants such as *Carex ensifolia* spp. *arctisibirica* and *Dryas punctata*, the generative cycle is complete throughout the zone.

One must bear in mind that only the visible phenological phases of vascular plants have been described above. The full generative cycle, however, is normally longer than one growing season (Gavrilyuk, 1961; Serebryakov, 1964; Deyeva, 1980; see also Chapter 2, this volume). Formation of flower buds begins in early spring and continues throughout the summer. The process ceases or slows down greatly in the autumn, but continues again the next summer. To reach flowering, the great majority of tundra plants need two growing seasons, and some of them, especially in snowbeds, need even more. The ripening of fruits may not even be completed by the end of one summer. In many species, it continues under snow during winter and sometimes also in the beginning of the next spring. Thus, for the completion of the full generative cycle, tundra plants may need more than three growing seasons, which means a total of about five months – that is, approximately the same time that is available during one growing season for plants in temperate zones. The observable phenological phases are the result of summing up processes occurring during several seasons.

All these remarks on vascular plants concern also numerous insect groups, which also need two or three years to complete their full development (Chernov, 1984a; see also Chapter 3, this volume). Larvae of some Tipulidae in the arctic tundra subzone have a developmental period of as much as five years (Lantsov and Chernov, 1987). The adaptations of plants and insects to the brevity of the vegetation period may be characterized as passive, because many species do not overcome this barrier.

In the middle of August, the peak number and the highest variety of species of pileate fungi are recorded (Stepanova and Tomilin, 1980), although

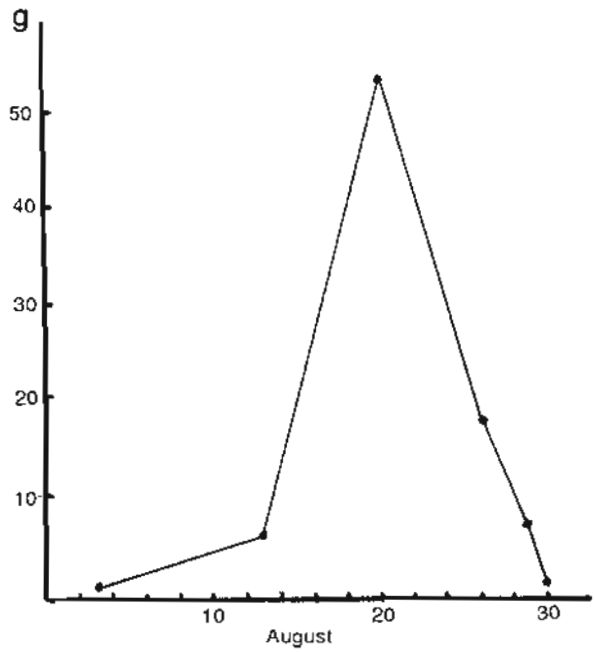


Fig. 16.83. Variation through August in biomass of macromycetes in the typical tundra subzone at Tareya, Taymyr, 1971. From Stepanova and Tomilin (1980).

a few species may be found in the tundra as early as July. After August 20, their numbers begin to decrease again, and at the end of the month only solitary examples can be found (Fig. 16.83). Because of a short growing period, there is only one crop of pileate fungi. The total biomass of macrofungi in the tundra, which is far lower than that in the forest zone (by a factor of almost one hundred), is strongly dependent on the meteorological conditions of the summer, especially in August. The governing factors which influence the development of the fungi are the temperature in the upper 5-cm soil layer, the precipitation, and the absence of frost.

A general decrease in bacterial numbers in the soil begins in the second half of August and they fall sharply in September (Parinkina, 1986). At the same time, the yeast populations increase during the entire growing season and reach a maximum just at the end of August (I. Chernov, 1985).

By the end of August, the air temperature falls considerably, and night autumn frost is usual. At this time, the plant colors are also drastically changed. The plant cover becomes most colorful in the forest tundra and in the southern tundra. Against a background of all possible shades of red produced by the leaves of the most widespread shrub, the dwarf birch (*Betula nana*), one can see yellow spots of shrub-willows and dwarf-shrub willows (*Salix glauca*, *S. polaris*, *S. pulchra*, *S. reptans*). Bog bilberries (*Vaccinium uliginosum*) are singled out by their lilac color, while the larches (*Larix*) look like yellow candles. Bright-red spots are formed by the clones of *Arctostaphylos alpina*, *A. rubra*, and *Rhododendron camtschaticum*.

In typical and arctic tundras, the autumn colors are not so spectacular. The leaves of the majority of grasses and herbs turn brown, only yellow willow leaves relieve the monotony of the general gray-brown background. The bright coloring of the tundra even in southern regions may last for only about one week. In the first 10 days of September, when snowfall may be frequent and frost is possible by day as well as by night, the growth processes stop in most species and the majority of the leaves die and/or drop. Afterwards the tundra, as in spring, acquires a dull grayish-brown coloring with a slight greenish shade due to some remaining leaves of semideciduous and evergreen plants whose growth slows or ceases.

At the end of September, there may be a full snow cover in many tundra regions. Mean daily temperatures below 0°C are often recorded about 10 days earlier. Thus, although growth in spring begins immediately after the disappearance of snow or even before, in autumn it ceases before new snow falls and even before the daily mean temperatures have become negative.

Autumn is the time when birds migrate to the south. Migrating flocks are recorded as early as the end of August, and the last birds leave the tundra in the middle of September. The reindeer begin to migrate to the south in the middle of August, although their main migration takes place at the end of August.

According to the calendar, the phenological autumn in the tundra ends in the first days of September (in polar desert at the end of August). Early autumn is marked by the onset of the day-night rhythm, the ripening of seeds in plants, and the migration of reindeer to the south. Late autumn is characterized by the seeding of plants, the autumn coloring, dying off of leaves, and the migration of birds.

The most important feature of the growing season in the Arctic is its brevity. Compared to temperate regions, it is reduced by about 2 months

in spring and by 1.5 months in autumn. In autumn, the growth of plants is completed before the actual critical conditions set in. The temperature regime up to the middle of September is not worse than at the end of June and the beginning of July, and the soil at this time is not frozen. Therefore, the growing season in the Arctic is 0.5–1 month shorter than the snowless period.

In spite of its brevity, the growing season has well-differentiated phenological seasons: spring, summer, and autumn. Each of them may be subdivided into shorter subseasons. The seasons and, especially, the subseasons are short, and they quickly replace each other. The shortest of them are the late-spring and early-summer periods, the longest are the early-spring and late-summer periods. The time of their onset and their duration depends on the meteorological conditions of the year and may vary markedly. In cold years, all phases of phenological development are prolonged. Many plants lengthen their period of prefloral development and budding. Breaking into blossom is very gradual, and the phase of seeding may not begin at all. In warm years, many species flower simultaneously. The general period of blossoming is shortened and the majority of species then normally complete their generative cycle by the autumn.

The dynamics of seasonal development during the growing season is most noticeable in the plant cover, but it is present in all groups of organisms. In anthophilous insects, it depends to a large degree on the developmental rhythm of the plant communities, in birds it depends directly on the weather conditions. Seasonal dynamics in the numbers and variety of taxa are also recorded in groups of soil invertebrates, as well as among the microbial populations of soil.

There is a certain degree of synchronism of the processes in arctic ecosystems. The period of highest temperatures, which usually falls within the last 10 days of July, coincides with a peak in the activity of almost all groups of organisms. This is the time of highest photosynthetic intensity, of maximum plant production, of maximum number of plant species in flower, and of a peak in hatching of nestlings, as well as the most active flight of insects and maximum bacterial production.

In spite of the brevity of the growing season in tundra ecosystems, the principle of variety in rhythms is also observed which ensures conditions for maintaining the relatively high biological diversity in the Arctic.

CENOTIC RELATIONSHIPS IN TROPHIC LEVELS OF ARCTIC ECOSYSTEMS

Studies on the interrelations between the organisms in tundras and polar deserts are very helpful for the better understanding of general laws of ecosystem functioning as well as for the development of a synecological theory. Biocenotic phenomena in the extreme conditions of high latitude are accentuated. For a synecologist, the communities of tundra and polar deserts, with their extremely low level of biological diversity and simplified structure, can represent the simplest model of an ecosystem – the same as a hydrogen atom for a physicist. Knowledge of biocenotic links and tropho-energetic processes in eecosystems of the Arctic is also very important for understanding the evolution of cenoses. The tundra landscape is considered "young", but the communities of high latitudes have quite a number of primitive and archaic characteristics. Such characteristics are especially well expressed in polar deserts where the features of primary terrestrial communities and the early stages of community evolution are clearly developed (Matveyeva and Chernov, 1976; Chernov, 1984b).

At the same time, the structure of communities and the character of cenotic links in tundras vary greatly in different parts of the tundra zone. That is why cenotic relations in tundra ecosystems must be studied as concretely as possible and any extrapolations must be done with much caution. The main initial factors that determine the specificity of tundra communities are general heat deficiency and brevity of the vegetative period. Secondary minor factors can also be distinguished that directly cause certain characteristics of cenotic relations:

(1) low primary productivity which declines sharply northwards, limiting the diversity and abundance of the consumers and the length of food chains;

(2) general decrease of the diversity of ecological factors, which restricts the number of possible niches;

(3) sharp reduction of the role of biocenotic factors and reinforcement of physical ones;

(4) extremely sharp latitudinal climatic gradi-

ents, existence of the tundra cenotic complexes in highly varied abiotic conditions;

(5) impoverishment of the chemical environment — general nitrogen deficiency in particular;

(6) very thin stratum of life where cenotic relations are developing; reduction of stratification and decline of the diversity of adaptive types of plants and animals related to different vertical strata;

(7) specific proportions of higher taxa within the arctic biota and in tundra communities (for example, increase in the ecological role of lichens and mosses); the diet properties of which are completely different from those of vascular plants;

(8) progressive reduction of taxonomic and ecological diversity, decrease in the number of candidates for this or that ecological "profession", one-species representation of many rich taxa and adaptive forms; and

(9) peculiarities of species structure of tundra communities and among them such phenomena as superdominance, and "shuffling" of the same set of species in the formation of communities and cenotic links.

Impoverishment of the tundra biota encompasses the taxonomic composition as well as the diversity of adaptive types, life forms, and functional units, "guilds", which compose the biocenoses. At the same time, the reduction of species richness, even extreme impoverishment of the group to a few or single species does not always cause a decrease in its role in performing its "own profession". A most characteristic example is that of the earthworms (Lumbricidae) as the most important group of sapro- and detritophages. In mixed, broad-leaved, subtropical and tropical forests, this group is represented by many species and plays an important role in the ecosystems. In most of the Siberian taiga and tundra zones mainly one, very plastic species occurs, *Eisenia nordenskioldi* (it is probably a complex of several closely related species). In tundras, *E. nordenskioldi* reaches very high numbers, sometimes higher than in the forests, and plays a significant role in the transformation of organic material (Striganova, 1985). In other words, in spite of extreme taxonomic impoverishment, the earthworms maintain their high biocenotic significance in Siberian tundras. The same situation is observed in the group of small herbivorous mammals (see below).

In some cases, certain features of life mode, which in southern biomes are not very pronounced in a given group of organisms, become more significant in tundra communities. For instance, winter gnats (Trichoceridae) in northern forests develop mainly in the litter and soil; sometimes they colonize the organic matter accumulated in rodent burrows. In the Arctic, they are numerous in different zoogenic substrates inside the holes of lemmings and arctic foxes, and on bird cliffs as well. The larvae feed on bacteria and fungi, which they take together with excrement and decaying plant residues. In tundras, this group is much more zoophilous and its number and general cenotic role are greater (see Lantsov and Chernov, 1987). Some craneflies, representatives of the family Tipulidae which is closely related to trichocerids, usually feed hardly at all in the imaginal stage or visit flowers occasionally. In the tundra, some other craneflies are active anthophils that feed intensively on the flowers (Lantsov and Chernov, 1987). It would be quite correct to refer to the same category such phenomena as winter food storing in some collared lemming (*Dicrostonyx torquatus*) populations (Dunaeva, 1978; Kiryuschenko and Kiryuschenko, 1979). One more example is the increase in the diversity of reproductive relationships in the Arctic including a greater variety of modes of entomophily in *Pedicularis* species (Chernov, 1978b; Williams and Batzli, 1982).

Some of the cases mentioned above can be considered as variants of a general ecological phenomenon of niche expansion when life conditions are sharpening and species richness is declining in the communities.

Trophoenergetic relationships

Primary producer level

The structure and functioning of biocenoses depend firstly on an autotrophic component – the first trophic level. In tundra vegetation, the share of vascular plants becomes lower, while the proportion of mosses and lichens is greater than in more southern biomes. The very significant role of moss turf in soil formation is well known in the literature; this turf maintains the heat and moisture regimes, determines the character of permafrost processes and serves as a habitat for numerous groups of organisms. The young shoots, meristems and roots of vascular plants are concentrated in the moss layer (Tikhomirov, 1952, 1963; Chernov, 1964; Tishkov, 1977; Chernov and Matveyeva, 1979).

However, the production indices of vascular plants in tundra communities are significantly higher than those of mosses and especially lichens. Thus, in southern shrub tundras in the northeast European part of Russia (in the Vorkuta region), the mosses in dry biotopes contribute at most 3% of the annual productivity aboveground, in moderately moist ones about 30%, and only in wetlands does this index reach 50%. The role of lichens in primary production is even smaller (see Table 16.24).

Vascular plants are not only more productive when compared with mosses and lichens, but more diverse in morphology, chemistry, and food properties too. It is only natural that they are more important for the consumers and for the formation of food chains in tundra ecosystems. Only a few of the tundra phytophages depend on mosses and lichens to survive (Chernov, 1985).

An important feature of the autotrophic component of terrestrial ecosystems of the tundra is the relatively very high proportion of algae, and even more of Cyanobacteria. Their cenotic role is particularly significant on the bare ground in different variants of polygonal and frost-boil tundras. The role of algae (taking into account the lichen component) is even more important in High Arctic communities, and in polar deserts they apparently dominate productive processes at the first trophic level. Correspondingly, the bulk of primary consumers in polar deserts are the animals feeding on algae (Chernov et al., 1977). Besides that, Cyanobacteria (settled on bare ground or plants, and also as lichen components) play a great role in nitrogen-fixing processes which are especially important in tundra ecosystems because of the general nitrogen deficiency (Grunina and Getsen, 1984a,b; Getsen, 1985).

TABLE 16.24

Annual aboveground production of the dwarf-shrub–moss phytocenoses in the vicinity of Vorkuta (g m^{-2} yr^{-1} dry weight)[1]

Plant group	Soil drainage			
	Good	Moderate	Weak	Swampy site
Vascular plants	105	90	111	85
Mosses	3	33	23	50
Lichens	2	1	1	0

[1]According to Vilchek (1986).

Primary production and, therefore, the energetic basis for the formation of trophic chains vary greatly from the southern to the northern limits of the tundra zone. Thus, on Taymyr, the annual aboveground productivity of vascular plants ranges from 90 to 130 g m^{-2} in southern and typical tundras, from 40 to 90 g m^{-2} in the northern part of typical tundras and in the southern part of arctic tundras, about 30 g m^{-2} in the northern part of arctic tundras, and about 5 g m^{-2} in polar deserts (Chernov et al., 1983; Vilchek, 1987). These figures are of the same order as those given by Wielgolaski (1986) from international tundra studies (see also Bazilevich and Tishkov, Chapter 17, this Volume).

In tundras and polar deserts, primary production fluctuates greatly depending on the nanorelief formed under the influence of cryogenic processes. The most productive elements of nanorelief are the well-heated rims around the patches of bare ground. The communities where such rims are well developed are the most productive ones. As is obvious from Table 16.25, patches of bare ground without moss cover may also represent a favorable habitat. This is the case in particular for vascular plants, due to the good conditions of soil heating. Some plants growing on bare ground have good vitality. Animal communities in frost-boil tundras are also very diverse in comparison with communities with a continuous moss cover (Chernov, 1978b).

The production indices vary greatly in accordance with micro- and mesorelief. Thus, productivity of herb–grass communities on south-facing slopes are two or three times greater than in zonal tundras. We have recorded the following values of annual aboveground productivity of vascular plants in different meadow communities: 72 g m^{-2} on the coast of Maria Pronchishcheva Bay, 146 g m^{-2} in the Dikson area, and from 200 to 400 g m^{-2} in the typical and southern tundra subzones (Chernov et al., 1983). Correspondingly the diversity and abundance of phytophages is known to be the greatest in herb–grass meadows (Chernov, 1973b).

For the evaluation of trophodynamic relationships, data on belowground productivity in tundra plants are very important. Attempts have been undertaken to estimate the increase of root biomass using indirect indices and making extrapolations on the basis of phytomass data. For instance, Vilchek (1986) has estimated the annual increase of European southern tundra subzone vegetation (be-

lowground parts) as about 20–50 g m^{-2}, which is only about 20–30% of aboveground productivity. Wielgolaski (1990) reports that the root production in polar desert is only one-quarter to one-half of aboveground production, while in southern tundra the main storage organs are normally the roots. However, one should take into account the fact that for consumers of roots in tundra communities the most important factor is not the productivity but the soil conditions, namely the temperature, humidity, aeration, density, and seasonal dynamics.

Phytophages

The diversity of typical phytophages decreases in the Arctic much faster than that of carnivorous, necrophilous, and saprophilous forms. This is not a specific characteristic of tundra communities, but rather a marginal manifestation of a general global regularity – the sharp decrease in taxonomical richness and diversity of adaptive phytophagous forms from the tropics to the poles (Chernov, 1992). This process can be followed easily within different animal taxa which include both phytophages and carnivores. For instance, the bulk of specialized phytophagous birds is concentrated in tropical forests. In the northern forest zone, there are still several groups of typical plant-eating birds, while in the Arctic, the typical phytophagous birds are represented by two species of Tetraoninae and a number of goose species. The most striking examples of adaptive radiation and the highest indices of taxonomical diversity and specificity, however, are found among typical carnivorous birds — for example, loons, gulls, waders, diving ducks, auks, etc.

A sharp reduction in the role of phytophages in the arctic fauna is clearly seen in two orders of Insecta: bugs (Heteroptera) and beetles (Coleoptera). Heteroptera are represented in the tundra zone mainly by two families, the phytophagous Miridae and the predaceous Saldidae. The Miridae is one of the biggest families (including about 650 species in the fauna of the entire former USSR). In the Eurasian tundra in general, only about 10 species of Miridae have been recorded; in typical and arctic tundras of Taymyr five species (Chernov, 1978b), and on Vrangel island two species (Khruleva, 1987). For the American Arctic as a whole, only eight species have been documented (Danks, 1981). In most cases, species of Miridae in tundra are not numerous and have a local distribution only. There are about 45 species of the family Saldidae in the fauna of the former USSR and about a quarter of this number occurs in the tundra zone. Among them are included such abundant species, widely distributed in the northern tundra, as *Calacanthis trybomi*, *Chiloxanthus arcticus*, and *Ch. stellatus* (Chernov, 1978b; Danks, 1981; Khruleva, 1987).

Of the numerous phytophagous families of Coleoptera, only snout beetles (Curculionidae) and leaf beetles (Chrysomelidae) are represented in the Arctic, with a score of one species each. Only two or three species of leaf beetles have colonized the "zonal" tundra communities, for example, *Chrysolina cavigera*, *Ch. septentrionalis*, and *Ch. subsulcata* (Chernov, 1973b, 1978b). Of this order, only three groups of predaceous beetles have colo-

TABLE 16.25

Total annual aboveground productivity of vascular plants in frost-boil tundras on Taymyr (g m^{-2} yr^{-1}, dry weight)[1]

Area	Zonal position	Patch of bare ground	Rim	Trough	Average per community
Cape Chelyuskin	Polar deserts	0	–[2]	13	5
Maria Pronchishcheva Bay	Northern part of arctic tundra	20	–	35	28
Dikson	Southern part of arctic tundra	43	–	32	38
Dikson	Southern part of arctic tundra	27	154	39	80
South of Dikson	Northern part of typical tundra	44	146	42	95

[1] According to Chernov et al. (1983).
[2] A dash means that the rim element of nanorelief is undeveloped.

nized the tundra environment successfully – ground beetles (Carabidae), diving beetles (Dytiscidae), and Staphylinidae – which account for about two-thirds of the coleopteran fauna of the tundra zone. It is worth mentioning that, in the northern forest belt, predaceous beetles make up not more than one quarter of the coleopteran fauna.

The more drastic northward reduction of species richness and diversity of the adaptive phytophagous forms, when compared with carnivorous ones, can be observed in very different groups – within the classes of mammals, birds, fishes, insects, etc. (Chernov, 1992). For the time being, it is impossible to explain the reasons of such correlations, particularly if the complex of saprophages and detritophages is not included in the analysis. Here, we can only put forward some suggestions.

First, the advantage of being carnivorous is obvious in respect of adaptation to the harsh and cold climate which demands higher energy expenditures. Second, numerous data lead one to think that carnivorous species are more capable of expanding geographically, and of forming vast ranges. At least among the terrestrial vertebrates, it is precisely the predators that have the largest ranges. This creates the preconditions for more intensive colonization of marginal arctic landscapes by predator forms of southern biomes. Third, the processes of speciation and adaptive radiation and the formation of a functional community structure with numerous niches in a severe climate and a reduced biodiversity are very specific. Perhaps the carnivorous mode of life itself maintains a higher rate of these processes in given environments. We may suggest that, in the process of distribution among niches, the diversity of the lower trophic level means less for carnivores than for phytophages. Evidently, for the processes of segregation of ecological niches at the third trophic level, the properties of consumers as such are more significant than anything else (for example, we invite the readers to consider the great role of different behavior responses). However, at the second trophic level the properties of food items, such as the chemical composition and morphology of plants or the structure of plant communities, are more important.

Now one more essential feature of the composition of the tundra biota should be mentioned. In more southerly biomes, including northern forests, the number of phytophagous species, even if the insects alone are considered, considerably exceeds the species richness of the flora. In the tundra zone, the correlation is reversed: the number of vascular plants is close to or even exceeds the number of typical phytophages (not taking into account the saprophilous species). This disproportion is especially prominent in the arctic tundra subzone where the number of phytophagous species, according to our counts on Taymyr and Vrangel Island (Khruleva, 1987), is always less than the number of vascular plant species. This difference is especially great in "plakor" tundra communities where the number of phytophagous species can be significantly lower than the number of vascular plant species. This fact must influence intensely the pattern of adaptive radiation and the interactions inside the system "plants–animals".

All the phytophagous birds and mammals of the tundra are able to eat a wide range of plants. However, due to the relatively small species diversity of the tundra flora in the diet of each animal species in a particular region or during a particular season, only a very limited number of plant species (or a single one) plays the leading role in their feeding habits. For example, tundra geese, the white-fronted goose (*Anser albifrons*) and the bean goose (*A. fabalis*), can eat very different plants, but more often their gizzards are stuffed with one or two species of grasses, for example, *Arctophila fulva*, cotton grasses (*Eriophorum vaginatum*, *E. angustifolium*), sedges (*Carex stans*), and sometimes *Equisetum arvense*. The most favorite food items for geese are the juicy parts of cotton grasses and sedges which are close to the roots and which the geese skillfully pull out of the moss turf. *Lemmus sibiricus* eats practically all the plants of tundra, but the bulk of its population lives on the fleshy plant parts – mostly sedges or in some places *Dupontia fisheri*, which are abundant in tundra where the harvest of the other grasses is too poor to feed the animals throughout a long winter.

Therefore, the range of available basic food items for tundra phytophages is strictly limited. Many authors concluded that tundra phytophages are more specialized trophically than the inhabitants of more southern landscapes. Thus, tundra lemmings are very often referred to as stenophages – that is, animals adapted to feeding on a strictly limited set of plants (Shwarts, 1963; Yudin et al., 1976). This is not, however, stenophagy, of course, but actually a result of a wide polyphagy – an ability to switch to the food items which are at any

moment the most available, most nutritious, and most abundant among those present.

During their migration across the tundra from the south to the north, reindeer change their diet composition many times. On Taymyr, on the breeding grounds in the northern parts of their migratory route, the role of grasses and various dicotyledonous herbs is very important. In southern tundra it is the role of the sedges, cotton grasses, and willows; in taiga areas in winter, it feeds mostly on lichens, especially on *Cladina stellaris* (Table 16.26). The high trophic plasticity of the reindeer reveals itself in its isolated resident populations on Novosibirskiye, Novaya Zemlya, and Sibiryakova islands. These islands lack shrubs, lichen tundras and meadow communities, and the productivity of vegetation cover is extremely low. In winter, shoot tips and buds of the dwarf willow *Salix polaris* and Brassicaceae were found in the stomachs of reindeer killed on the Novosibirskiye islands (Kishchinskyi, 1971). It is amazing that a deer manages to satisfy its hunger with such tiny plants.

The most abundant passerine birds of the northern tundra (*Calcarius lapponicus*, *Eremophila alpestris* and *Plectrophenax nivalis*) are typical polytrophic species. In spring in tundra, they may feed on seeds, insects, or both; in summer they eat more insects; and in late summer they usually turn to seeds and other parts of a wide range of plants. For many tundra birds, it is rather characteristic to switch their diet to the food items which are most abundant and available at any particular time. Thus, in southern tundra, in years when there is a rich harvest of cloudberry (*Rubus chamaemorus*) these berries become the main food for many birds, e.g., puddle ducks (Anatinae), ptarmigans (*Lagopus*), skua gulls (*Stercorarius*), and geese.

At the same time, distinct interspecific differences in food preferences and food spectra have been revealed among phytophages. For example, *Lemmus sibiricus* is conservative in its diet composition and has close connections with the dominant tundra plants, the sedges. According to a number of authors, however, this lemming also eats green mosses readily (Fig. 16.84). Nevertheless, this can be determined by the peculiarities of preferable biotopes rather than by food preferences as such. For an example, *L. sibiricus* has closer relationships with genuine tundra communities than *Dicrostonyx torquatus* (Fig. 16.85), which is more closely associated with various herb–grass and dwarf-shrub communities. The diet of *D. torquatus* is more diverse, with a greater quota of dicotyledonous herbs and dwarf-shrubs.

A good example of substantial differences in the diet of very close species is provided by the two *Lagopus* species: willow (*L. lagopus*) and rock (*L. mutus*) ptarmigans (Table 16.27). Though the sets of food plants have very much in common, the diet of these two species differs considerably at different seasons. For instance, in winter the willow ptarmigan feeds on willow twigs, whereas the rock ptarmigan uses alder catkins and buds.

In spite of the relative uniformity of the diet of tundra phytophages, substantial variations in different regions and subzones have been observed. The basic adaptive strategy of the trophic links of tundra vertebrate phytophages is to vary these relations according to the current conditions. This is a manifestation of a potential polyphagy, the ability to use a variety of foods depending on the season, weather, life cycle phase, or the amount of the food supply.

Among the insects, there are also quite a number of typical polytrophic species connected with a wide spectrum of tundra plants. Included are many lepidopterans – for example, the large tussock

TABLE 16.26

Ratio of food items (%) in the diet of wild reindeer of Taymyr in different seasons[1]

Food items	Summer	Early autumn	Late autumn	Winter	Early spring	Late spring
Lichens	4.5	12.5	22.7	36.6	32.4	11.7
Grasses	53.0	48.7	43.2	41.4	44.2	66.2
Shrubs	31.5	16.6	6.9	5.6	8.4	7.2
Dwarf-shrubs	2.9	10.1	8.2	6.6	6.6	5.2
Mosses	6.5	6.7	7.9	5.8	4.1	8.3
Others	1.6	5.4	11.1	4.0	4.3	1.4

[1] From Syroechkovskyi (1986).

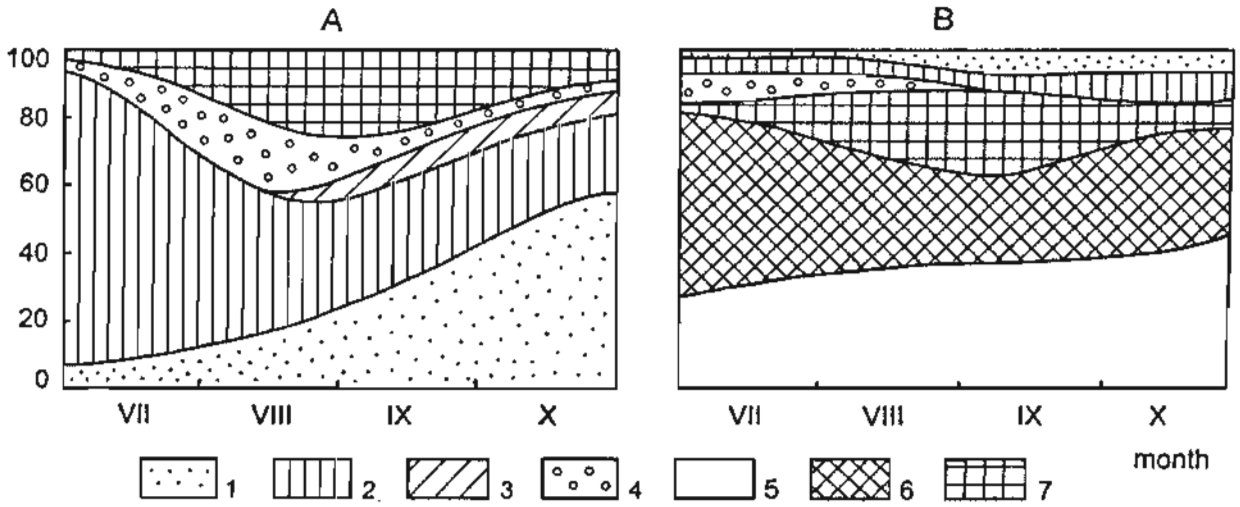


Fig. 16.84. Changes (%) in components of the diet of two lemming species on Vrangel Island. A, *Lemmus obensis*; B, *Dicrostonyx torquatus*; 1, mosses; 2, sedges; 3, cotton grasses; 4, grasses; 5, willows; 6, *Dryas* spp.; 7, herbs. From Kiryushchenko and Kiryushchenko (1979).

moth (*Gynaephora lugens*), whose hairy caterpillars live openly on the surface of sedge and moss turfs. Many leaf beetles are also typically polytrophic, especially the commonest among tundra species, *Chrysolina septentrionalis*. However, the fauna of phytophagous insects include a significant proportion of oligophages, strictly connected with certain plant taxa. Such typical oligophages include tundra leaf beetles from the genus *Chrysomela*, that feed on willow leaves. In fact, in some species the monophagy manifests itself in a clear preference for one food species. For instance, *C. taimyrensis* develops mainly on *Salix arctica* (Fig. 16.86), although this beetle can feed on other willow species as well (Chernov, 1973b).

Various species of the sawfly subfamily Nematinae are also associated with the willows. Here, we again can see cases of facultative monophagy. For example, gall-forming larvae of *Pontania crassipes* on Taymyr settle on all the willow species, but obviously prefer *Salix reptans*. Many species of arctic lepidopterans are oligophages; for example, the owlet moth *Polia richardsoni*, common in Siberian tundras, is associated with dwarf-shrubs, *Colias* species with legumes, *Erebia* and *Oeneis* with grasses, some tube moths with shrubs, and others with wormwood (*Artemisia*).

Therefore, along with polytrophic species that are as common among the tundra insects as they are among vertebrates, the typical oligophages have certain advantages in the arctic environment, their trophic relations having, in the course of evolution, been strictly assigned to certain plant taxa.

Another problem is specialization of phytoph-

Fig. 16.85. Lemming *Dycrostonyx torquatus*, descendant of steppe rodents in arctic fauna.

TABLE 16.27

The ratio of food items in the diet of willow ptarmigan (*Lagopus lagopus*) and rock ptarmigan (*L. mutus*) on Taymyr (mean values for a year, %)[1]

Plant	Willow ptarmigan	Rock ptarmigan
Dryas leaves	12	10
Betula nana buds and leaves	23	7
Leaves, buds and twigs of willows	44	2
Alder buds and catkins	1	77
Seeds and berries	10	2
Other material	10	2

[1] According to V.M. Pavlov's data in Chernov (1985).

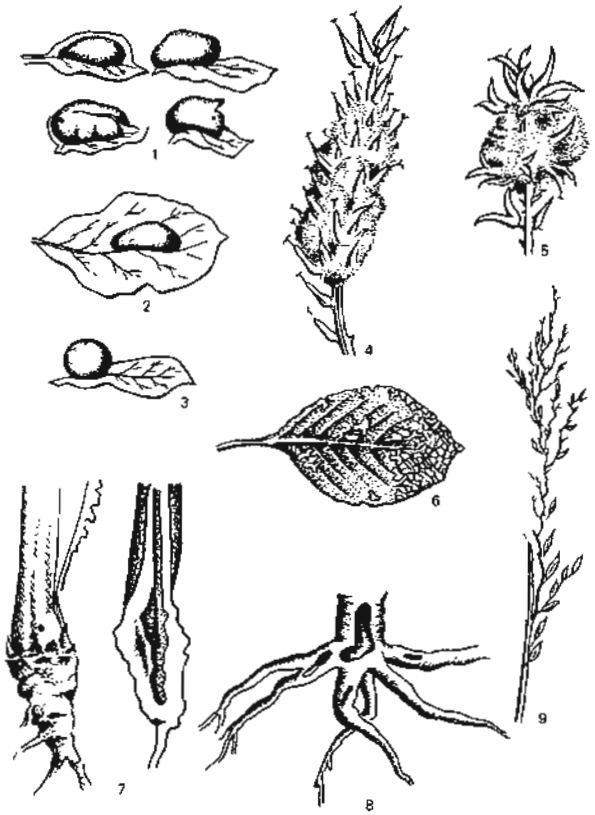


Fig. 16.86. Typical insect pests on plants in Taymyr. 1–3, galls on willow leaves made by the sawfly *Pontania crassipes*; 4–5, catkins of arctic and creeping willows (*Salix arctica*, *S. reptans*) damaged by the larvae of the sawfly *Pontopristia*, 6, leaves of arctic willow (*Salix arctica*) damaged by larvae of the leaf cutter *Chrysomela taimyrensis*; 7, roots of *Pedicularis oederi* damaged by larvae belonging to the fly family Muscidae; 8, roots of another lousewort (*P. dasyantha*) damaged by caterpillars of the tortricid moth *Olethreutes*; 9, grass spike of *Poa arctica* damaged by the carabid beetle *Amara alpina*. From Chernov (1985).

ages with respect to the plant parts they feed on. In general, leafeaters (phyllophages) dominate among phytophages. In the tundra zone, this complex also predominates in the number of species, but is still very much impoverished. The most characteristic feature of the tundra complex of phyllophages is the very pronounced reduction of sucking phytophage species, especially of colonial ones (Aphidinea, Coccinea). Only very few species of sucking phytophages among the bugs, cicadellids and psyllids, are distributed up to the northern limits of the typical tundras; single species, such as bugs of the genus *Orthotylus* and the cicada *Hardya youngi*, penetrate into the arctic tundras (in the north of Taymyr and on Vrangel Island). Locusts are practically absent from the tundra complex of phyllophages. Only one species, *Melanoplius frigidus*, is widely distributed in forest tundra, but never reaches the real tundra. Therefore, in the complex of tundra phyllophages all groups of insects with incomplete metamorphosis (Hemimetabola) are extremely reduced due to the peculiarities of their ontogeny and of the development of their eggs (Chernov, 1978a).

The basis of the phyllophagous complex in Siberian tundras consists of three groups of insects with complete metamorphosis (Holometabola): Tenthredinidae, Lepidoptera, and Chrysomelidae. Lepidopterans predominate in the number of species, while the larvae of the Tenthredinidae are the leaders in the number of individuals and in biomass. On Taymyr, in dry sedge–moss tundra, tenthredinid larvae represent up to one-third of the total biomass of grass dwellers, and in communities with shrub willows and dwarf birchs they sometimes make up the bulk of zoomass. In meadow communities on south-facing slopes, their proportion is significantly lower, while the biomass of chrysomelid larvae is sometimes very high, especially that of *Chrysolina septentrionalis*.

The tundra complex of rhizophages (root-eaters) is severely reduced. In genuine tundra biotopes, in sedge–moss tundras, they are practically absent. In mixed herb–grass–meadow communities, on the other hand, a number of typical rhizophages occur, having the characteristic adaptive features of this life form. Included are the caterpillars of the tube moths *Olethreutes inquinatana* living on the roots of *Pedicularis dasyantha* (Fig. 16.86) and *Eucosma guentheri* on the roots of wormwood (*Artemisia*). In meadow communities, the nodule snout beetles *Sitona* are common in some places where they settle on the roots of different legumes. On south-facing slopes, large weevil larvae of the genus *Lepyrus* developing on willows are sometimes abundant. The larvae of different dipterans (Cecidomyiidae, Anthomyiidae, etc.) are also common on the roots of many plants.

Carpophages (seed- and fruit-eaters) are represented in tundra communities by various taxa with considerable species diversity. For example, a rich complex of species is associated with willow fruits. On Taymyr, the fruits of *Salix arctica, S. pulchra*, and *S. reptans* are heavily damaged by sawflies of the genus *Pontopristia*, and, apparently, a particular sawfly species develops on each willow species. In southern tundras, weevils of the genus *Dorytomus* are associated with willow catkins. Seeds

of many species of dicotyledons, grasses, and cotton grasses are the food of cecidomyiid larvae. Larvae of flies (Anthomyiidae and Muscidae) have been found in inflorescences of some Asteraceae, especially those of *Saussurea tilesii*. Larvae of Diptera heavily infest the fruits of *Pedicularis* (*P. hirsuta*, *P. oederi*, *P. sudetica*). Another diverse complex of carpophages is associated with legumes. We found the larvae of the weevil *Phytonomus ornatus*, various galls of the family Cecidomyiidae, and caterpillars of microlepidopterans in inflorescences and fruits of *Astragalus subpolaris*, *Oxytropis middendorfii*, and *O. nigrescens*. Weevils of the genus *Apion* feeding on seeds are common as well. A facultative but abundant carpophage is the ground beetle, *Amara alpina*, which climbs the plants at "night" and feeds on the ovaries and ripening seeds of various plants, grasses in particular (Fig. 16.86).

The carpophagous insects maintain their cenotic potential in tundras to a much greater degree than other trophic groups of phytophages. Obviously, the secret life inside compound fruits and the rich diet help to maintain the relatively high diversity level of this trophic group in tundra communities.

A diverse complex of insects is associated with flowers as pollinators. This aspect is outside the scope of this paper. Some insects feed on flowers or their parts and may be referred to as anthophages. In tundra, a typical example is the small chrysomelid, *Hydrothassa hannoverana*, that eats the petals and stamens of buttercups (*Ranunculus*) and *Caltha arctica*. The pollen together with pollen sacs of many plant species are eaten by sawflies, in particular the large forms of the genus *Tenthredo*.

The relationships between phytophagous insects and different groups of tundra plants are very diverse. A complex of species developing on willows is very rich and includes numerous saw flies of the subfamily Nematinae that feed on leaves and fruits, weevils feeding on catkins and roots, chrysomelids, butterfly caterpillars, Psyllidae, dipterans, and bumblebees feeding on pollen, etc. In fact, insects feed on every part of willows. Numerous insects are also associated with legumes: weevils (*Apion* feeding on seeds and *Sitona* on root tubercles), caterpillars of Tortricidae, *Colias*, and other lepidopterans. Various phytophages feed on Asteraceae — for example, caterpillars on roots, chrysomelids on leaves, and fly larvae inside the fruits. Fruits and roots of *Pedicularis* are also damaged heavily.

At the same time, the fauna of phytophages feeding on such important tundra plants as Brassicaceae, Caryophyllaceae, and Cyperaceae is rather poor. Only few fly species of Chloropidae and Cecidomyiidae forming galls use the great variety of tundra herbs.

The bulk of phytophages are concentrated in meadows, herb–dwarf-shrub communities, and shrub habitats on the slopes. On the other hand, in typical "zonal" communities, in *Dryas*–sedge–moss tundras, the numbers and species diversity of phytophages are low. They are represented here mainly by a number of sawfly species, microlepidopterans, cicadellids, and a few species of phytophagous mites.

Concluding this short review of trophic links between insects and plants, one has to underline the extremely limited knowledge of biocenotic aspects of these relationships. However, various links in the system "insects–plants" in tundras could become excellent models for understanding the principal problems controlling population dynamics, mechanisms of the segregation of ecological niches, and the general pattern of ecosystem homeostasis.

The impact of phytophages on plant communities

In spite of their low diversity, primary consumers still have such summary parameters of productivity and energy budgets as correspond with their place in the trophic pyramid. At the same time, the sharp decline in the diversity of phytophages in tundra and the fact that quite a number of phytophagous groups or taxa are represented by few species undoubtedly must influence the pattern of trophodynamic processes. In this paper, we already put forward the idea that, when the number of species is minimal, their total population density is often considerably higher than in a multispecies community because of the higher reproduction rate of some species. This is, perhaps, one of the consequences of a disturbance or inadequate rigidity, of the mechanisms which control the growth of populations. One is dealing with an analogous phenomenon when one studies the complex of tundra phytophages.

The population density of two lemming species (*Dicrostonyx torquatus*, *Lemmus sibiricus*) and the magnitude of their impact on the tundra vegetation are extremely large. There are no other biomes where one could observe the same large-scale and

regular removal of primary production by the consumers. Actually, in Eurasian tundras, the lemmings devastate their food supply completely every three or four years, when their population outbreaks take place (Chernyavskyi and Tkachev, 1982). According to different authors, during the periods of peak populations lemmings consume from 20 to 70% of the phytomass (Batzli, 1975; Tishkov, 1977; Kiryushchenko, 1979). The range of annual consumption of vegetation by lemmings is given in Table 16.28.

The scale of food consumption by lemmings in tundra vegetation is very different in winter and in summer. *Lemmus sibiricus* on Taymyr, during its summer population peak, takes about 15% of the aboveground phytomass of vascular plants and in winter up to 34% of the total plant material, including mosses (Orlov, 1985).

It is common opinion that tundra lemmings do not feed on mosses deliberately, but swallow them occasionally or take them as ballast food (Dunaeva, 1948). Special investigations have shown that *L. sibiricus* feeds on certain species of hypnoid mosses rather willingly (Fig. 16.84); in particular, on Vrangel Island it consumes *Tomenthypnum nitens* (Kiryushchenko and Kiryushchenko, 1979). In these authors' experiments, the lemmings ate only the very tips of moss shoots. That is why they could not satisfy their hunger even by eating a large number of moss shoots, and died if they could not find some other food. *Dicrostonyx torquatus* eats mosses only as an occasional food.

Mosses are not a nutritious food, having only secondary value in the diet of *Lemmus sibiricus*. At the same time, during a population outbreak, the impact of lemmings on tundra moss cover is enormous. In winter, living under the snow, they have to literally gnaw their way through the moss turf to get the succulent, next-to-root parts of other plants hidden in the moss thicket, thus clipping off huge amounts of moss. Therefore, in their sites of winter feeding, a solid "carpet", consisting of clipped mosses mixed with the remnants of vascular plants and lichens, could often be found. At the same time, the lemmings do not touch the most compact, frozen turf which becomes more and more compact and thicker every year, being strengthened with the shoots of sedges and *Salix polaris*, forming small hummocks amidst the sites where lemmings continuously clip off the mosses and vascular plants. Thus, the distinctive nanorelief with small hummocks is formed (Fig. 16.87). Such sites are rather common in the arctic tundra subzone on Taymyr.

Another result of the winter feeding of lemmings is the concentrations of "lemming hay" (Fig. 16.88) – the remnants of the upper, less valuable parts of grasses, sedges, and cotton grasses, that lemmings deposit as "left-overs". This garbage, being washed out by the melted snow, mixes with other plant residues and forms dense swaths on the gentle slopes of river shores. This peculiar analogue of forest litter serves as a habitat for very varied small saprophilous invertebrates (springtails, mites, larvae of dipterans, beetles, etc.). The latter evidently play an important role in the formation of humus and soil.

At this point, a great number of difficult questions arise concerning populations, biocenology, productivity/energy budget, and evolution. We will consider only one of them: how such a strong physical impact of phytophages affects the plant community. Is it always a catastrophe for the phytocenoses? Does it always lead to their degradation?

TABLE 16.28

Dynamics of phytomass and amount of elements consumed by lemmings (both *Dicrostonyx torquatus* and *Lemmus sibiricus*) in tundras on western Taymyr[1]

Year	Biomass of lemmings ($g\ m^{-2}$)	Amount consumed		
		Phytomass ($g\ m^{-2}$)	Nitrogen ($kg\ ha^{-1}$)	Mineral elements (P, K, Ca, Mg) ($kg\ ha^{-1}$)
1967	0.02	22.6	0.4	1.9
1969	0.09	151.8	2.4	7.1
1970	0.54	649.0	10.0	21.5
1971	0.04	36.1	0.6	0.9

[1] From Tishkov (1977).

Fig. 16.87. Hummock nanorelief under lemming influence in *Salix polaris*–sedge–moss wet community at Dikson, Taymyr. A, general view; B, close view.

There are some grounds to suggest that the regular removal of large amounts of vegetation by lemmings can be considered as one of the mechanisms regulating primary productivity. Thus, experiments carried out on Vrangel Island (Kiryushchenko, 1979) have shown that herbs and grasses, strongly affected by *Lemmus sibiricus*, increased their aboveground phytomass production considerably in the next year. However, heavily damaged shrubs and dwarf-shrubs, constituting a food supply mainly for *Dicrostonyx torquatus*, decreased in productivity. Certain experiments gave us evidence that the feeding activity of lemmings (large-scale consumption of tundra vegetation) and the dynamics of production processes are well balanced, and that considerable damage to the plants should not be considered as a destruction of food supply but rather as a mechanism of increasing it before the next lemming population outbreak has begun (Tishkov, 1977).

Some available data suggest the existence of autoregulation mechanisms within the system: "lemmings–vegetation" (Fig. 16.89). Such mechanisms include processes stimulating rapid restoration of the vegetation cover: for example, reduction in the efficiency of thermal insulation of moss turf, increase in thawing depth of the permafrost and amelioration of the soil hydrothermal regime, fertilization of the soil with feces and carcasses of lemmings, etc.

The picture described above is characteristic for the typical and arctic tundras. In southern tundra, the lemming population cycles are less pronounced and the scale of their biocenotic impact is reduced. Also, in such tundra, the lemmings do not have the position of absolute dominance within the complex of small rodents. There are other numerous and widely distributed species, including Middendorf's vole (*Microtus middendorffii*), the narrow-skulled vole (*M. gregalis*), the tundra vole (*M. oeconomus*), and several others. The overall synecological effect of their activity in the southern part of the tundra zone and in forest tundra is, nevertheless, smaller than in northern tundras.

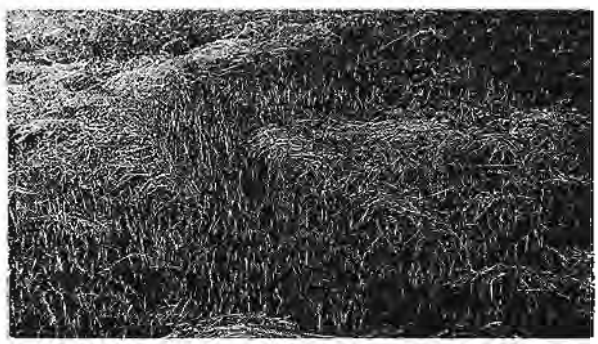


Fig. 16.88. Lemming "hay", the remnants of winter lemming feeding brought together by melting water in spring.

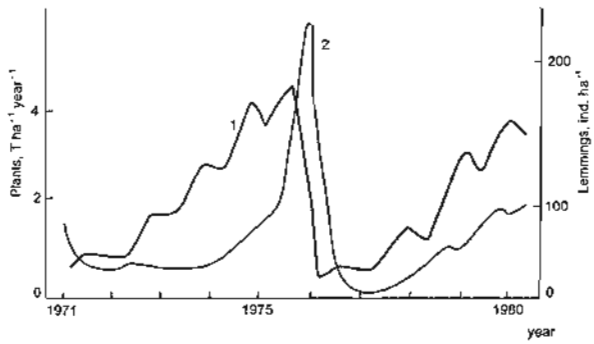


Fig. 16.89. Relationship between (1) primary production and (2) the numbers of *Dicrostonyx torquatus* on Vrangel Island. From Orlov and Sarancha (1992).

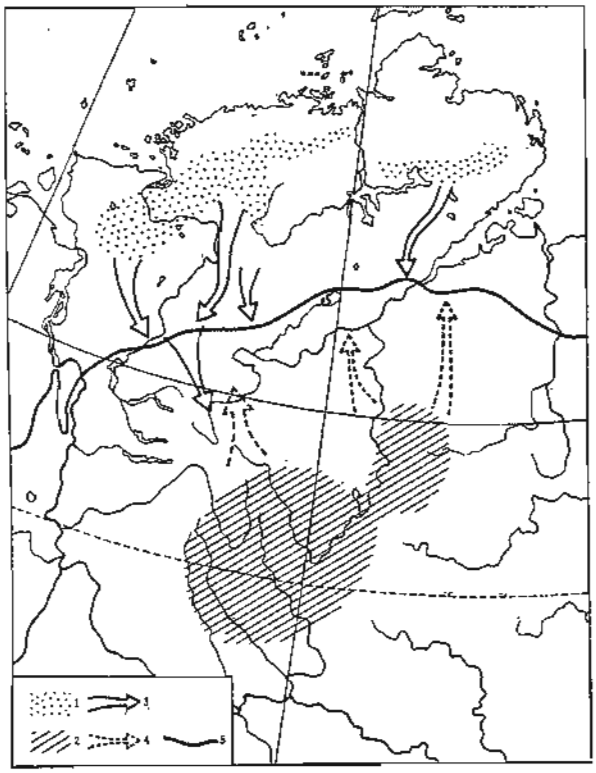


Fig. 16.90. Annual life cycle of the Taymyr herd of reindeer (*Rangifer tarandus*). 1, Calving grounds and concentration during summer; 2, basic wintering area; 3, autumn migration route southwards; 4, departure form wintering grounds; 5, limit of the tundra.

The dynamics of the system "lemmings–vegetation" is usually considered in the literature as very characteristic of tundra ecosystems. At the same time, there are no examples of such large-scale effects on vegetation due to other tundra consumers. Great damage to the pastures by reindeer grazing occurs mainly in the case of domesticated deer, and deer husbandry is developed only in forest tundra and forest regions. As to wild reindeer, as far as one can judge by the existing herds on Taymyr, for instance, they have well-developed mechanisms of shifting use of food supply (dispersal of grazing animals across vast territories and short stay at each site). During its annual life cycle, the Taymyr herd of wild reindeer covers a territory of about 1,000,000 km^2 (Fig. 16.90). Winter, calving, and grazing grounds during autumn, spring, and summer migrations are located in different regions covering a huge area, and grazing and migration grounds change through time: in one day a herd may walk about 100 km. Therefore, though the population numbers of wild reindeer in Taymyr are about 500,000 animals, nowhere has intensive trampling or grazing damage been observed, and only about 2% of the annual phytomass increase is taken by the reindeer (Kolpashchikov, 1989). Only in certain places – along the lake shores, in narrow land-bridges between the lakes, or in river crossings – are permanent trails formed, and moss turf heavily trampled by the reindeer (Fig. 16.91).

A certain cyclicity of population dynamics of wild reindeer is very possible, but must certainly be a long-term one. Perhaps the current numbers of the Taymyr population are a result of its intensive growth since the early 1950s. It is noteworthy that the population grows, or, at least, maintains its high numbers in spite of the very intensive hunting that started in early 1970s. At present, up to 90,000 animals are harvested yearly from a total population of 600,000. There are reasons to believe that without hunting, which is a limiting factor preventing overpopulation, the Taymyr population would reach its maximal size and its natural decline would begin.

The greatest impact the reindeer exert is on the lichen communities which represent their principal winter feed supply. The most valuable for reindeer winter feeding are lichens of the genus *Cladina*, especially *C. stellaris* which forms a dense cover in some places in mountain tundra, forest tundra, and northern taiga. Excellent feeding sites covered by fruticose lichens exist on the Kola peninsula, where a resident population of reindeer lives on a nature reserve, and also in Evenkiya where the Taymyr population spends the winter. To reach lichens covered by snow, the reindeer have to dig deep pits. Only in the sites where dense lichen "carpets" are developed can a deer be satiated. The productivity of lichen sites is relatively low, about 700 kg ha^{-1} yr^{-1}. In one year, a lichen thallus increases its length by only 4.8 mm. By biting the lichens, a deer removes a 10-year increase of the thallus. That is why in places of intense winter grazing by reindeer the lichen cover is absolutely exterminated in 3 or 4 years. Other variants of vegetation appear in their place; for example, grasses. Only after a 5-year break does effective regrowth of the lichens start, and it takes 15–20 years to restore the cover on a heavily damaged site. In summertime, fires occur rather often in such lichen communities, and then they can be restored completely only in 70 years (Semenov-Tyan-Shanskyi, 1977).

Fig. 16.91. Wild reindeer on Taymyr during autumn migration southwards. Photo by A. Krechmar.

However, catastrophic consequences occur only in the case of domesticated reindeer grazing if protective measures are not taken. The wild reindeer have many features which prevent rapid destruction of winter pastures: grazing only during the period of most severe frosts and maximal snow cover, quickly moving to the summer pastures, etc.

Another group of vertebrate phytophages that create a certain pressure on tundra vegetation are the geese. In Siberian tundras, two species of geese are especially numerous: the white-fronted goose (*Anser albifrons*) and the bean-goose (*A. fabalis*). In some areas, other species are common as well (*Anser erythropus*, *Branta bernicola*, *B. ruficollis*, *Cygnus bewickii*). On Vrangel Island, a large colony of snow geese (*Chen hyperboreus*) is well-known. The characteristic tracks of geese feeding in tundra were noted by people many years ago (see Tikhomirov, 1959). These birds eat cotton grass with particular delight, pulling the plants out, biting off the succulent part which is next to the roots, and throwing away the other part. In some places, large areas are covered with such "left-overs" mixed with droppings, probably greatly influencing the dynamics of cotton-grass stands. Geese also willingly eat other succulent plant parts, skillfully searching the moss turf for sprouts (probing the turf with their beaks, pulling out the sprouts, and leaving numerous holes and moss scraps in the turf). In autumn, before the migration, the geese gather into large flocks, usually leaving on their feeding sites barren patches with 100% damaged vegetation, trampled and covered by excrement. The problem of the impact of goose grazing on the productivity of tundra communities has been discussed in the literature repeatedly, based on data collected in Greenland and northern Canada (Madsen, 1988). Unfortunately, no attempts have been made so far to study the scale and details of these phenomena in Siberian tundras and to evaluate them from an ecophysiological point of view.

Regular outbreaks of phytophagous insects are known for northern forests and forest tundra. For

example, the larch leaf-rolling moth, *Zeiraphera griseana*, in eastern Siberia periodically causes great damage to subarctic larch forests. They also invade tundra in large numbers and can be met even on the arctic sea ice. In Scandinavia and on the Kola peninsula, outbreaks of the autumnal moth, *Oporinia autumnata*, have been observed, and heavy damage to birch stands at the tree line has been registered. On territories with typical tundra cover, the density of phytophagous insects never reaches such a level that their impact on plants could be comparable with the effects of lemmings. We can only refer to the already given examples of heavy local impact of insects on certain organs of plants (Fig. 16.86). But these impacts have exclusively local importance and do not significantly affect the phytocenoses as a whole.

Returning to the lemming cycles, one must admit that such large-scale damage to vegetation is a phenomenon known not only in the tundra zone; it is just a particular case of a pattern of population dynamics which can be observed in many phytophagous species in other landscapes, including forests. However, it is indisputable that, in tundra conditions, population dynamics of this type and its biocenotic consequences are expressed especially strikingly. Nowhere else do the life activities of one or two species lead to such powerful and catastrophic biocenotic consequences, reflected in all the different links of the ecosystems.

Saprophilous complex

The performance of primary consumers is only one of the links in the system of relationships between first and second trophic levels. In the energy flow of an ecosystem the role of the saprophilous complex of organisms connected with the substrate consisting of dead plant residues is very important. This complex represents the bulk of the soil animal population. While much reduced in diversity, this complex is a leading component of animal communities in the tundra zone. In terms of biomass, soil saprophilous invertebrates play a leading role throughout the humid climatic belt, and are by one order of magnitude ahead of phytophages and several orders ahead of predators. In terms of total population numbers, biomass, and metabolism rate, five groups of invertebrates are the most important within tundra communities: Enchytraeidae, Lumbricidae (mostly *Eisenia nordenskioldi*), Nematoda, Collembola and larvae of Tipulidae. Less important in this complex are oribatid mites, one of the most important groups of saprophages in the forest zone (Table 16.29). In different communities, the number of saprophilous larvae of various dipterans (Sciaridae, Mycetophilidae, Muscidae, etc.) is sometimes rather considerable. An important feature of the saprophilous complex of high latitudes is the decline in diversity of true saprophages or primary decomposers — the animals directly consuming dead, but not yet decayed, plant parts. Thus, the typical saprophages (larvae of Bibionidae, which inhabit forest litter in great numbers) in the Siberian Arctic are common only in southern shrub tundras where they feed on shrub leaf litter: in typical tundras, they are very rare and in arctic tundras completely absent. Another group of true saprophages, the millipedes (Diplopoda), are completely absent from the tundra zone.

A characteristic feature of the majority of invertebrates in the tundra saprophilous complex is polytrophy — the combination of such modes of

TABLE 16.29

Weight (g m^{-2}) of different groups of saprophilous invertebrates at Tareya, Taymyr[1]

Animal group	*Dryas*–sedge moss tundra	Moss rims in frost-boil tundra	Bare ground in frost-boil tundra	Herb–*Dryas* communities	Herb–grass meadows
Nematoda	1.20	1.02	0.78	4.20	7.70
Enchytraeidae	1.00	1.66	4.93	13.90	25.69
Lumbricidae	2.00	1.99	4.18	26.00	60.00
Oribatei	0.10	0.13	0.06	0.20	0.10
Collembola	1.53	0.86	0.35	0.86	2.22
Tipulidae (larvae)	0.30	0.40	0.52	0.40	3.68

[1] From Chernov (1978b).

feeding as saprophagy, detritophagy (eating of highly decayed residues and soil), different forms of microphagy (bacteriophagy and mycophagy), and algiphagy, which is especially characteristic for the inhabitants of high-latitude tundras and polar deserts (Chernov et al., 1977).

In this respect, the earthworms (*Eisenia nordenskioldi*) and tipulid larvae are the most striking examples of broad polytrophy (Striganova, 1982, 1985; Lantsov and Chernov, 1987). An example of typical polytrophy is the larvae of the cranefly *Tipula carinifrons*, abundant in frost-boil tundras. They eat plenty of dead leaves, especially of the dwarf-shrub *Salix polaris*, but also living tissues of grasses, dwarf-shrubs, mosses, and algae. Moreover, there are some reasons to suggest necrophagy, the feeding on dead invertebrates. At the same time, the morphology and histology of the *T. carinifrons* intestine are typical for saprophages (Lantsov and Chernov, 1987).

For many groups of invertebrates of the saprophilous complex of the tundra (various larvae of dipterans, springtails, earthworms, enchytraeids), detritophagy and microphagy are also more typical than true saprophagy.

The process of decomposition of plant residues in the tundra proceeds with a marked lack, or a complete absence, of large animals – primary decomposers which serve as a major factor in intensifying the transformation of plant material through reducing the substrate to small fragments, fermentation, and activation of the bacterial flora. The role of bacteria in the process of transformation of organic compounds in the tundra decreases sharply northward. Bacterial activity is especially heavily suppressed in arctic tundras and polar deserts. Thus, in the southern part of tundra, the bacterial production in summer is several times greater than production of aboveground plants, while in the arctic tundras and polar deserts these two estimates are rather close (Table 16.30). This leads to an accumulation of undecomposed plant residues and a general suppression of the vigor of vegetation and serves as one of the barriers preventing the formation of continuous vegetation cover in arctic tundras and polar deserts (Matveyeva and Chernov, 1976; Parinkina, 1989). In comparison with the forest belt, the diversity of important taxonomic and functional groups of microorganisms in tundra soils is decreased, the groups most reduced being actinomycetes, spore-forming bacteria (genus *Bacillus*), and higher basidiomycetes – that is, the groups including many species with a high rate of hydrolytic activity, a powerful enzymatic apparatus, and an ability to decompose complex and almost inaccessible organic compounds (polymers, polysaccharides, aromatic compounds, humus). In soils of more southerly latitudes, the representatives of these groups are mostly responsible for the final stages in the destruction of organic matter. In tundra soils, groups such as asporogenic rods, yeasts, *Mucor*, and imperfect fungi – characteristically saccharolytic organisms – have the greatest cenotic weight. From the successional point of view, the microflora of tundra soils as a whole is rather a "pioneer" one, having a more pronounced saccharolytic function (decomposition and utilization of easily accessible compounds like simple saccharides, organic acids, amino acids, etc.).

The role of bacteria is particularly small at early stages in the decomposition of plant litter. Thus, in Parinkina's (1989) experiments in the Taymyr tundras, the bacterial flora did not play an important role during the first year of litter decomposition. Only in certain cases did large numbers of bacterial decomposers of cellulose develop during the first year of experiment, for example, when legume litter was tested. It is well known that decomposition of these plant residues is particularly rapid.

In the process of primary biological transformation of plant litter in tundra ecosystems, the fungi play an important part; they are often able to maintain physiological processes at low temperatures (Flanagan and Bunnell, 1980; Parinkina, 1989). Due to their diverse and powerful enzymatic apparatus for decomposition of highly stable substrates, and also to the intensive spatial growth of

TABLE 16.30

Some parameters of the productivity of bacteria in comparison with vascular plants on Taymyr[1]

Parameter	Typical tundras	Arctic tundras	Polar deserts
Annual aboveground productivity of vascular plants (g m^{-2})	89.6	27.0	5.1
Monthly production of bacteria (July) (g m^{-2})	242.0	26.0	7.5
Ratio of "living" phytomass to dead mass	1:0.18	1:0.90	1:4.3

[1] From Parinkina (1989).

TABLE 16.31

Number of yeasts and mycelium fungi (thousands of cfu g^{-1}) at different stages of decomposition of the leaves of two plant species in the same plant community of a typical tundra on Taymyr[1]

Substrate	*Dryas punctata*		*Carex arctisibirica*	
	Yeasts	Fungi	Yeasts	Fungi
Green leaves	181 ± 12	14 ± 4	224 ± 21	7 ± 1
Dead leaves	490 ± 44	217 ± 21	296 ± 23	326 ± 15
Decaying leaves	55 ± 16	256 ± 26	15 ± 2	304 ± 19

[1] From I. Chernov (1985).
cfu, colony-forming units.

their colonies, fungi have an undeniable advantage over bacteria, particularly in the initial stages.

In the Taymyr tundras, associations of single-celled fungi were investigated, i.e. yeasts connected with various plant substrates (Bab'eva and Chernov, 1982; I.Y. Chernov, 1985). Yeasts are capable of growing intensively at low temperatures, and among them there are obligate psychrophilic forms. In low temperature conditions, yeasts compete successfully with other saccharolytic fungi for the fresh plant substrate. They develop abundantly on leaves, whether living, dying, or dead (but not yet decayed). On green leaves, their number exceeds the quantity of mycelium fungi by one or even two orders of magnitude (Table 16.31). All the species of yeast isolated in tundra, including *Cryptococcus laurentii*, the most abundant in various biotopes, actively utilize different oligosaccharides, their derivatives, and organic acids, but are unable to use polymers. Evidently, the main function of yeasts in tundra ecosystems is the accomplishment of the earliest stages of transformation of organic compounds.

In the course of decomposition as the reserves of accessible carbohydrates run low, the substrate is actively colonized by mycelium fungi, while the number of yeasts declines (Table 16.32). Thus, another type of yeast association is formed which is characteristic of soils. However, its dominating species are also not able to utilize polymers actively.

The rate of decomposition of dead plants in tundra depends not only on climatic conditions and saprotrophic organisms, but on the structure and chemistry of plant tissues as well (Table 16.33). Taymyr vascular plants can be arranged in the following order, according to the decreasing rate of mass loss of their litter: legumes, sedges, grasses, shrub leaves and dwarf-shrub leaves (Parinkina, 1989).

It is only natural that the reproduction and performance of microflora are very different in various biotopes, depending on humidity, soil structure, and heating intensity (Table 16.34). The influence of soil invertebrates (earthworms, enchytraeids, springtails, mites, larvae of dipterans, nematodes, etc.) on the activity of saprotrophic organisms is enormous. In biotopes where the diversity and biomass of soil animals are maximal, the population of microorganisms is also extremely rich and the decomposition of plant litter is most intensive. Thus, on south-facing slopes on Taymyr with dark soil with a well-developed A_1 horizon ("turf"), herb–grass vegetation, and a maximal level of zoomass (up to 90 g m^{-2}), the taxonomic composition of the microflora also shows great diversity. In such soil, these microor-

TABLE 16.32

Number of yeasts (thousands of cfu g^{-1}) on different substrates in various communities in the arctic tundra subzone on Taymyr[1]

Substrate	Frost-boil tundra (*Salix polaris*)	Mire (*Carex stans*)	Dry slope (*Dryas punctata*)
Green leaves	493 ± 111	394 ± 31	850 ± 100
Dead leaves	564 ± 83	973 ± 34	168 ± 19
Decaying leaves	14 ± 2	No data	19 ± 4
Soil (cm) 0–2	9 ± 2	3 ± 1	0.9 ± 0.4
2–10	0	0.4 ± 0.1	0

[1] From I. Chernov (1985).
cfu, colony-forming units.

TABLE 16.33

The rate of leaf decomposition in the southern tundra subzone on Taymyr – losses in mass (%) during the first two years after shedding[1]

Plant	First year	Second year
Astragalus subpolaris	54.0 ± 4.1	68.6 ± 1.9
Betula nana	34.1 ± 2.2	40.4 ± 2.3
Grasses (several species together)	22.8 ± 2.3	45.3 ± 1.3
Salix pulchra	19.2 ± 2.2	29.7 ± 1.2
S. reptans	30.7 ± 1.4	38.4 ± 1.6

[1] From Parinkina (1989).

ganisms undergo intensive development as ammonifiers, nitrogen-fixing forms, actinomycetes, bacterial decomposers of cellulose, etc. The development of bacteria is more intensive in heaps of animal excrement as well as in the intestine. For example, the enzymatic system of *Eisenia nordenskioldi* facilitates the decomposition of cellulose in the intestine, where the bacterial decomposers of cellulose become more active (Kozlovskaya, 1976).

In the intestine of earthworms and tipulid larvae, polymers are formed such as humic acids. Humification of the organic material continues in earthworm casts and in cranefly excreta. For example, under the lichen crusts on a patch in frost-boil tundra where the numbers of *E. nordenskioldi* and *Tipula carinifrons* are high and where large amounts of their casts and excreta are accumulated, the humification level of organic material reaches 60%. On surrounding sites with dense moss turf, the humification level can be about 20% (Vasilevskaya, 1980). At the same time, there is a hypothesis that in tundra the activity of invertebrates can slow down the decomposition of litter — for instance, as a result of microarthropods feeding on fungi (J.W. Whittaker, 1974; Luxton, 1982).

The processes of death and decomposition of mosses in tundra are still very little known. So far, one can only state that mosses decay very slowly (Berg, 1984). Mosses do not form litter, in the common meaning of the word. Their dead parts stay on the growing plant for a long time without contact with the soil. Moss "litter" is very poor in nutrients, especially in nitrogen, and contains plenty of compounds that prevent decomposition and suppress the growth of microorganisms. One of the reasons for this is the very small content of lipids in mosses (Pakarinen and Vitt, 1974). In moss turf, many small invertebrates, live, springtails in particular, but they feed mostly on fungi and algae. One can assume that in the process of moss decomposition the main role is played by fungi.

According to Parinkina's opinion (1989), the process of litter transformation in tundra includes successive steps of physical breakup, alkalization, and primary biological decomposition of plant residues by fungi during late autumn and early spring, and subsequently the inclusion of secondary decomposers (detriphages and microphytophages) which facilitate the establishment of closer contacts of microorganisms with the substrate. These secondary decomposers also promote the activity of microflora, which supplement the enzymatic activity of animals and complete the mineralization of organic residues. Parinkina (1989) believed that low soil temperatures do not represent the direct and main factor in the slow decomposition of litter in the tundra, because a significant part of the arctic microflora consists of psychrotolerant forms, and the activity of the latter at positive temperatures is usually the same (when calculated per unit of time) as that of numerous thermophilic forms in other types of communities. Thus, in some biotopes of frost-boil tundras and herb–grass meadows, bacterial production during one summer month can reach 500 g m^{-2}. The main factor in the low overall effect of the activity of microorganisms is the shortness of the period during which they are active.

Among the factors inhibiting processes of decomposition of organic compounds in the tundra are (1) the chemical composition of litter, which contains plenty of highly stable compounds suppressing the growth of microorganisms (particularly the dead parts of mosses and dwarf-shrubs), (2) the absence or low number of typical sapro-

TABLE 16.34

The rate of leaf decomposition in the typical tundra subzone on Taymyr – losses in mass (%) during the first year after shedding[1]

Plant	Frost-boil tundra		Polygonal mire	
	Patch of bare ground	Moss rim	Moss rim	Wet depression
Dryas punctata	6.3 ± 1.2	24.2 ± 4.6	–	–
Salix reptans	8.2 ± 2.1	38.2 ± 1.4	–	–
Carex stans	32.7 ± 1.0	45.7 ± 3.9	39.7 ± 4.5	50.0 ± 2.8
Betula nana	44.1 ± 0.9	47.6 ± 0.5	41.2 ± 1.3	49.1 ± 2.3

[1] From Parinkina (1989).

phages and primary decomposers among invertebrates, which is also a factor in the low activity of the bacterial population, particularly of cellulose reducers, and (3) the relatively low abundance of fungi playing the main role in the processes of biological decomposition of litter. At the same time, in spite of the general reduction in the activity of saprophytic microorganisms and the insignificant level of chemical weathering in tundra soils, the microorganisms represent the principal agents for releasing the mineral nutrients from plant tissue.

The level of carnivorous animals

The complex of carnivorous forms in the Arctic is rather diverse. It has been impoverished to a lesser degree than described above for the phytophagous fauna. This relative diversity of the carnivorous forms when compared with phytophages undoubtedly causes the peculiarity of relationships at the third trophic level. One of the peculiar features is a concentration of many predatory species around a few species of prey and their synchronous population dynamics. This phenomenon has been carefully studied by Osmolovskaya (1948) on the Yamal peninsula, using the complex of predators feeding on lemmings as a model. Later, the same characteristic feature of food links of tundra carnivorous animals was confirmed for the insectivorous birds (Chernov, 1967). This is a reflection of one of the most important features of species composition of tundra communities — the superdominance mentioned above. It can be considered as a simplification of the organization of tundra ecosystems, but at the same time it creates an extremely powerful and rigid mechanism of control of population dynamics within a complex of correlated species.

The most important part of the third trophic level is a complex of vertebrates feeding on insects and other invertebrates. In the tundra zone, it consists almost exclusively of birds. In all natural zones except the Arctic, the passerines are the absolute dominants among insectivorous birds. In the tundra, the majority of bird species feeding on invertebrates are waders (Charadrii), which often also predominate by numbers in "zonal" communities (Chernov, 1978b; Stishov et al., 1989). This can be explained, probably, by the advantages of the nidifugous type of development over the nidicolous type (where the chicks stay in the nest for a long period) and also by the feeding mode of the waders – probing the moss cover with their bills. Passerine birds are incapable of such behavior (Chernov and Khlebosolov, 1989).

Studies of the trophic links among arctic insectivorous birds began more than two decades ago on Taymyr (Chernov, 1967). Later, a series of papers devoted to the same problem were published by Kishchinskyi (1976, 1978), Khlebosolov (1983, 1986), and others who worked in the southern part of Eurasian tundra zone. The main direction of these investigations is the analysis of mechanisms and strategies for the use of food resources by insectivorous birds, by means of the concept of segregation (division) of ecological niches.

Two groups of insects play especially important roles in the feeding of arctic birds, namely, Chironomidae and Tipulidae. Aquatic larvae of chironomids form the bulk of the diet of arctic ducks of subfamily Aythynae. The waders eat the terrestrial larvae of chironomids (especially in polar deserts), and both waders and passerines feed on their imagines. Tipulids are especially important in the diet of tundra waders, which eat all developmental stages (Table 16.35). Tipulid larvae play a most important role in the diet of waders in spring, after their arrival in the tundra. Cases are known of clear food preferences for the larvae of certain tipulid species. For example, the curlew sandpiper (*Calidris ferruginea*) especially willingly picks up the larvae of *Tipula carinifrons* from the patches of bare ground in different types of frost-boil communities. In many cases the gizzards of these birds are stuffed with the larvae of this one tipulid species. Marsh species of waders search for the larvae of *Prionocera* most actively. The passerines eat great numbers of tipulid imagines, but certain species successfully feed on their larvae as well.

In spite of significant similarity in the diet composition of adult insectivorous birds, there are some reasons to suggest that their food niches have been divided sufficiently on the basis of different relations with habitats and different techniques of catching the insects. The food spectra of chicks are much less similar. In waders, it is mostly the result of clear segregation of preferred sites for brood feeding (Table 16.36).

In passerine birds, rather significant differences in the composition of chick diets have been observed among different species (Table 16.37). Only a few groups of invertebrates (spiders, chironomids) are represented in the food items

TABLE 16.35

Quantity of tipulids and other insect groups (mean number of specimens per stomach in the diet of adult waders (Charadrii) in the northern part of Taymyr

Food item	*Pluvialis squatorola*	*Pluvialis dominica*	*Arenaria interpres*	*Calidris ferruginea*	*Calidris alba*	*Calidris maritima*
Prionocera spp., larvae	0.6	2.0	1.6	3.0	3.1	6.0
Tipula glaucocinerea, larvae	7.0	0.3	9.6	1.4	4.6	1.3
T. carinifrons, larvae	3.6	1.6	1.8	2.6	0.5	0.5
Other *Tipula* spp., larvae	1.0	0	0	0.2	0.4	0.3
Tipulidae, pupae	0	0	8.0	0	0.4	1.0
Tipulidae, imagines	5.3	5.0	0	0.3	3.4	5.5
Other insects	2.3	11.3	11.2	5.0	9.8	17.8

brought to the nests of almost all species of tundra passerines. The insects of quite a number of taxonomic groups (Psyllidae, Cecidomyiidae, pupae and larvae of Tipulidae, imagines of culicid mosquitoes, butterfly caterpillars, etc.) are exploited only by single bird species. Naturally, the differences in chick diet will be greater if one compares the species of the invertebrates they eat.

The reasons for the differences in diet composition are rather various. In the case of passerine chicks, such factors are the place and mode of feeding used by the parents. For example, psyllids inhabiting willow catkins are eaten only by redpolls (*Acanthis flammea*) while bluethroats (*Luscinia svecica*) hunt successfully for tipulid larvae since they are able, as all Turdidae, to search forest litter and soil for insects. Table 16.38 illustrates yet another example: the amount of beetles with different morphological characteristics in the food of three species of waders. These waders use similar feeding biotopes in the southern tundra where the insect fauna is rather rich and the available food is much more diverse than in northern tundras. It is only natural that the richer the available diet is, the more diverse the factors will be on which food niches are segregated.

Many authors who have studied the food links between birds and insects in tundra put forward the problem of the tension of these relationships and try to determine how great is the pressure of consumers on populations of their prey species. The data concerning the proportion of the prey population consumed by entomophages are rather contradictory. In comparison with the total estimate of biomass of invertebrates, the requirements of entomophages are relatively modest. The point is, however, that a bird does not actually get all the food it could theoretically eat. Khlebosolov (1986) conducted experiments fencing the broods of pectoral sandpipers (*Calidris melanotos*) on plots with different supplies of available food. It was shown that, for the successful growth of chicks, a sufficiently high abundance of chironomids (300–500 imagines m^{-2}) is needed. However, if the chironomids on a certain plot are very abundant but small in size (about 0.2 mg each), the chicks cannot catch them effectively (Holmes, 1966; MacLean and Pitelka, 1971). Evidently, these chicks need a

TABLE 16.36

Preferred feeding sites for wader broods in lower reaches of Kolyma River[1]

Sites	*Calidris melanotos*	*Calidris acuminata*	*Philomachus pugnax*	*Limnodromus scolopaceus*	*Pluvialis dominica*
Lake shores, mire edges	+	–	–	–	–
Mesic sedge–moss mires	–	+	–	–	–
Wet sedge–moss mires	–	–	+	–	–
Shallow pools and lakes	–	–	–	+	–
Dry "plakor" tundras	–	–	–	–	+

[1] From Chernov and Khlebosolov (1989).

TABLE 16.37

Diet composition[1] of passerine nestlings according to data obtained by the use of neck bands[1]

Food item	*Motacilla flava*	*Anthus cervinus*	*Luscinia svecica*	*Emberiza pusilla*	*Acanthis flammea*	*Phylloscopus trochilus*
Aranei	+	+	+	+	+	–
Psyllidae	–	–	–	–	+	–
Lepidoptera, larvae	–	–	–	–	+	+
Tipulidae, imagines	+	+	–	+	+	–
Tipulidae, larvae	–	–	+	–	–	–
Tipulidae, pupae	–	–	–	+	–	–
Chironomidae, imagines	+	+	+	–	+	+
Culicidae, imagines	–	–	–	–	–	+
Cecidomyidae, larvae	–	–	–	–	+	–
Tenthredinidae, imagines	–	–	–	+	–	–
Tenthredinidae, larvae	–	–	–	–	+	+

[1] Food items composing less than 15% of the diet were not taken into account.
[2] From Chernov and Khlebosolov (1989).

certain concentration of sufficiently large chironomids (1–4 mg each). When the number of chironomids was about 100 m^{-2}, the growth of chicks was slowed down, they clearly lacked the amount of food they needed and their energy costs were no longer covered by the food they could get. Only one of four chicks in this case was still growing normally, while the others perished. According to Khlebosolov's observations, in years of unfavorable weather conditions and low chironomid numbers, three chicks died and only one survived in a majority of pectoral sandpiper broods.

TABLE 16.38

Quota[1] of different morphological groups of beetles in the diet of three species of waders in the "plakor" tundra on southern Yamal[2]

Groups of beetles	*Pluvialis apricarius*	*Numenius phaeopus*	*Limosa lapponica*
Large, shining, mobile	++	+	+
Large, dim, mobile	+	–	–
Large, dim, not mobile	+++	+++	+
Medium, shining, mobile	++	–	+
Medium, dim, mobile	+++	+	+++
Medium, dim, not mobile	+	++	–
Small, shining, mobile	+	–	–
Small, dim, mobile	+++	+	++

[1] Categories: +, frequency in the stomach up to 10%; ++, up to 20%; +++, over 20%
[2] From Andreyeva (1989).

Khlebosolov's field experiments can be related to the size of the nesting territory protected by males. It was shown that its area is approximately equal to, or greater than, the minimal area needed for feeding the chicks of one brood. Khlebosolov calculated that one brood (4 chicks) of pectoral sandpipers demands a territory of 4 ha or more, and that the territories the males begin to defend in spring range from 4 to 8 ha. Nesting sites of another species (*Limnodromus scolopaceus*) are much larger, from 30 to 90 ha. In the feeding of this species, the hydrophilic oligochaetes, Enchytraeidae and Lumbricidae, dwelling in small shallow pools amidst the dry tundra play a special role. In each nesting territory, there must be a certain and sufficient number of such pools.

Evidently, since the diet composition of tundra waders is so very diverse and changeable, their chicks can grow successfully only if the density of certain invertebrates is high enough that the amount of food obtained by the chicks exceeds their energy expenses. The distribution of such a food supply determines the nesting density of these waders. This is because the abilities of the chicks to switch to another kind of prey are poor and their stereotype of food reactions is very pronounced. It is obvious that, for the successful breeding of waders, such food items as emerge in the tundra every year in great abundance and stay for a relatively long period (sufficient to let the chicks mature) are especially important.

The main problem usually arising when the

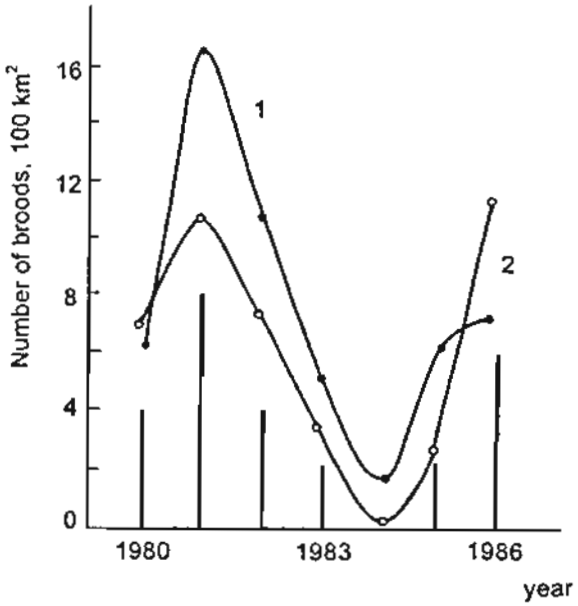


Fig. 16.92. Breeding intensity of 1, arctic fox *Alopex lagopus* and 2, snowy owl *Nyctea scandiaca* and the numbers of lemmings (columns with scale from 0 to 4) on Vrangel Island. From Litvin and Ovsyanikov (1990).

relationships predator–prey are under consideration is: how are the dynamics of interacting populations controlled? In this respect, the system predators–lemmings is especially representative, being, since the time of Shelford's works, a classical model for studying the mechanisms of biocenotic control. In recent years, interesting investigations have been conducted in the tundra zone of Russia dealing with the relationships between predators and lemmings — for example, on Vrangel Island (Chernyavskyi and Tkachev, 1982; Chernyavskyi and Dorogoi, 1988; Litvin and Baranyuk, 1989; Litvin and Ovsyanikov, 1990, and others), on Yamal (Kalyakin, 1989), on Taymyr (Orlov and Sarancha, 1992), and in other regions.

In tundras in the northeastern part of Europe and Siberia, the population dynamics of *Dicrostonyx torquatus* and *Lemmus sibiricus* are quite synchronous and have a clear cycle pattern with a period of 3–5 years. The next maximum comes at least in 3 years. The rises and declines are expressed most clearly in the arctic tundra subzone and in the northern part of the typical tundra subzone — for example, on Vaygach Island, in the north of Taymyr, and on Vrangel Island – that is, in the regions where lemmings are the only murid rodents. In southern parts of the tundra zone and also in forest tundra, the fluctuations in the numbers of lemmings and other rodents are rather less significant (Kalyakin, 1989). The reasons for this phenomenon are not quite clear; we propose the general level of biological diversity. In southern tundras, there are several other species of small rodents besides lemmings, such as *Clethrionomys rutilus*, *Microtus gregalis*, *M. middendorfii*, and *M. oeconomus*. The diversity of predators is greater as well. These factors make the ecological niches narrow, enlarge the potentialities of biocenotic control of population dynamics, reduce the danger of sharp rises and drops in numbers due to reduction of food supply, and facilitate the stability mechanisms of ecosystems.

It is natural that the food specialization of different species of predators and their dependence on lemmings are different. Four species of predators are strongly connected with lemmings: arctic fox (*Alopex lagopus*), snowy owl (*Nyctea scandiaca*), pomatorhine skua (*Stercorarius pomarinus*), and rough-legged buzzard (*Buteo lagopus*). The pomatorhine skua breeds only in the years of peak lemming populations. During the intervening periods, it may still occur in the tundra but, as a rule, does not breed. Reproduction of the arctic fox also strongly depends on the number of lemmings (Fig. 16.92); but this polyphagous predator is able to hunt lemmings even when their density is very low, and also to use a wide spectrum of substitute food items such as bird eggs, chicks, carrion, human hunting and food wastes, and even bumblebee nests which this fox constantly searches for, digs out and eats. That is why, even in years of low numbers of lemmings, some couples breed pups successfully. Fluctuations in the reproduction rate of snowy owls are greater than in arctic foxes. When the numbers of lemmings decline, the size and number of owl clutches reduces sharply, and on vast tundra territories not a single living nest of this bird is found (Osmolovskaya, 1948; Litvin and Ovsyanikov, 1990). The breeding of the rough-legged buzzard also depends greatly on the numbers of lemmings. As early as Osmolovskaya's work (1948), data were given showing a sharp decline in the nesting density of this species in tundra after the numbers of lemmings had been reduced. This species rarely nests in the arctic tundra – mostly in typical and southern tundras, where its diet also includes voles and many bird species.

The population number of long-tailed skua (*Stercorarius longicaudus*) is also connected with

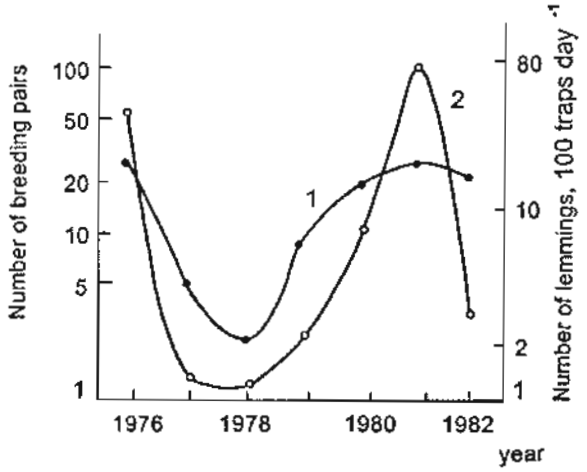


Fig. 16.93. Dynamics of the numbers of 1, long-tailed skua (*Stercorarius longicaudus*); 2, lemming (*Lemmus sibiricus*) on Vrangel Island. From Chernyavskyi and Dorogoi (1988).

the number of lemmings, but this polyphage breeds successfully during the periods of their lowest numbers as well (Fig. 16.93).

The correlations between the lemming cycles and two species of small mustelids, the weasel (*Mustela nivalis*) and the ermine (*M. erminea*), have not yet been properly studied.

The species involved in this "suite" of lemming predators differ not only in general specialization of their diet. They also use the lemmings in different ways during different phases of their population cycles (Fig. 16.94). Thus, on Vrangel Island, during the peak of lemming numbers, the pomatorhine skuas eat more lemmings than any other predator, taking about 50% of all lemmings eaten by predators. At the stage of population growth, the main consumer of lemmings is the snowy owl, and during decline and depression of lemming population the arctic fox (Chernyavskyi and Dorogoi, 1988). Ermines and weasels eagerly catch and eat lemmings under the snow in winter. In summer, the ruined nests of lemmings can be met rather often – the "left-overs" of fox meals. So far, there are no reliable data on the proportion of lemming populations withdrawn by these predators.

In the phase of their peak population, lemmings are eaten by many animals, even by those that do not usually hunt small rodents, such as the peregrine falcon (*Falco peregrinus*). At this time, even reindeer eat them. The arctic chars (*Salvelinus alpinus*) also eat a lot of dead lemmings, whose bodies lie on the shores and on the ice cover of water bodies or have been washed away by melted ice and snow. Sometimes, the stomachs of these fishes are literally stuffed with lemmings. In the years of high lemming numbers, the glaucous gull (*Larus hyperboreus*), arctic skua (*Stercorarius parasiticus*), and herring gull (*Larus argentatus*) also feed on lemmings, as do the gyrfalcon (*Falco gyrfalco*), white-tailed eagle (*Haliaëtus albicilla*), raven (*Corvus corax*), and some others in the southern part of the tundra zone.

The total number of lemmings withdrawn from their populations varies greatly at different stages of their population cycle (Figs. 16.95, 16.96). Increase in their number stimulates more intensive predation by the growing number of predators, whose reproduction rate increases causing greater food requirements. The maximal quota of lemming populations is consumed during the periods of their maximal numbers. So far it is unclear what the maximal level of consumption of prey population by the predators is. Chernyavskyi and Dorogoi (1988) have given an estimate of 20% for the population of Vrangel Island. Kalyakin (1989) believed that relationships in the predator–lemming system are much more tense. According to his calculations, the consumption rate can reach 90% in the south of the Yamal peninsula (Fig. 16.97).

Concepts concerning the role of predators in the dynamics of lemming populations are very contra-

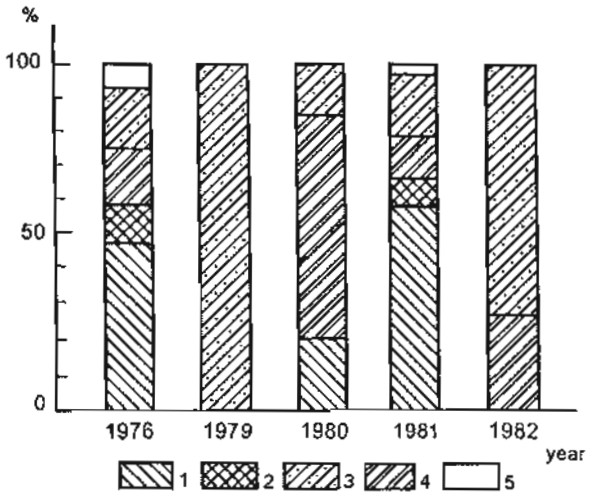


Fig. 16.94. Relative amount of lemmings caught by predators at different phases of population cycle on Vrangel Island. 1, *Stercorarius pomarinus*; 2, *S. longicaudus*; 3, *Alopex lagopus*; 4, *Nyctea scandiaca*; 5, *Larus hyperboreus*. From Chernyavskyi and Dorogoi (1988).

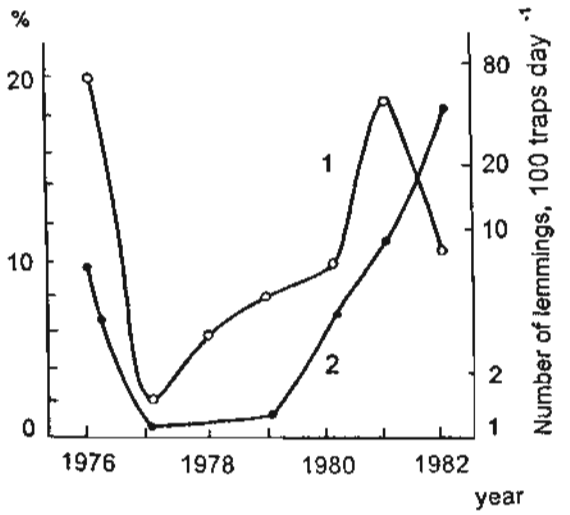


Fig. 16.95. Dynamics of the number of 1, *Dicrostonyx torquatus*; 2, % of its population removed by predators on Vrangel Island. From Chernyavskyi and Dorogoi (1988).

dictory. In particular, it is still unclear if predation can be considered as a regulatory factor acting according to the feedback principle with a certain amount of automatism. Many authors believe that predators are the main factor causing the decline in lemming numbers after the peak, or even the principal factor in their population cycles (Shelford, 1943; Pitelka et al., 1955; Koshkina, 1970; Kalyakin, 1989). Other authors think that different groups of predators play essentially different roles in lemming population dynamics – for example, birds of prey just "cut off the upper part" of lemming populations, while further reductions

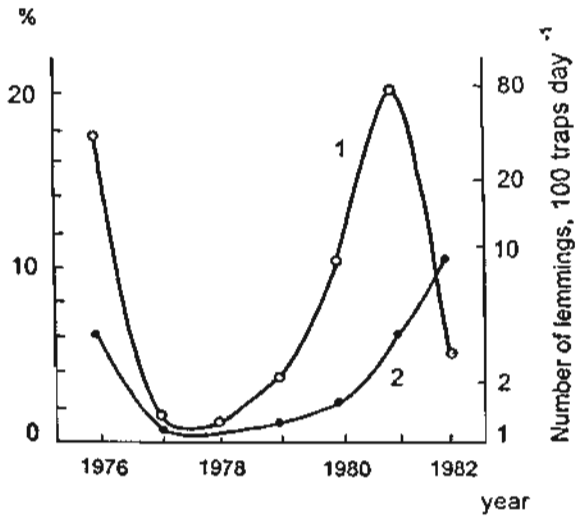


Fig. 16.96. Dynamics of numbers of 1, *Lemmus sibiricus*; 2, % of its population removed by predators on Vrangel Island. From Chernyavskyi and Dorogoi (1988).

depend on the performances of the arctic fox, ermine, and weasel (Pearson, 1966; MacLean et al., 1974). However, long ago Krebs (1964) noted that predator pressure should not be considered as an obligate part of population cycles of lemmings. This point of view was shared by Chernyavskyi and his coauthors (Chernyavskyi and Tkachev, 1982; Chernyavskyi and Dorogoi, 1988). In their opinion, the dynamics of lemming numbers are controlled by the population factors acting according to the feedback principle. In particular, the main causes of population decline following the peak of lemming numbers are considered to be the decrease of reproduction rate, the increase in juvenile mortality, etc. Predation in this context is considered as a modifying phenomenon facilitating the reduction of population number, and no more than that.

In our opinion, in different zonal conditions (in polar deserts, in arctic, typical, and southern tundras), the correlations between factors controlling

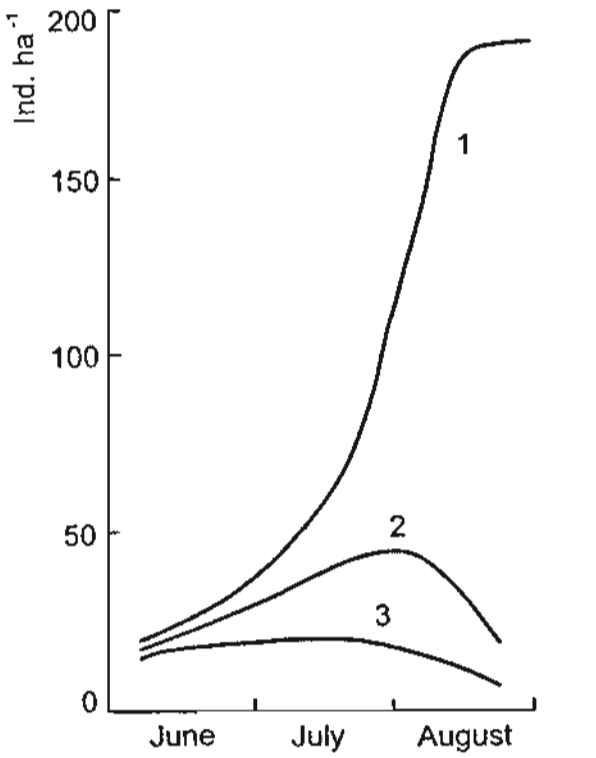


Fig. 16.97. Pressure of birds of prey on populations of *Dicrostonyx torquatus* and *Lemmus sibiricus* on southern Yamal. 1, probable changes in lemming population density under pressure of predators; 2, maximal consumption of lemmings by birds of prey; 3, the remaining lemming population. From Kalyakin (1989).

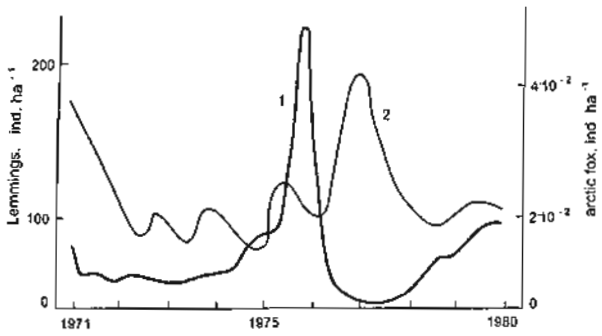


Fig. 16.98. The model of long-term dynamics of numbers on Vrangel Island. 1, lemming (*Dicrostonyx torquatus*); 2, arctic fox (*Alopex lagopus*). From Orlov and Sarancha (1992).

the lemming population dynamics can be very different too. In particular, there is no reason to describe as contradictory the situations known on Vrangel Island and Yamal (Figs. 16.95–16.97). Most likely, they represent the different modes of performance of the predator–prey system in different climatic and biocenotic conditions, such as different levels of biological diversity responsible for regulatory functions in the ecosystems.

It is absolutely obvious that birds of prey and mammals, together with lemming populations, constitute a typical co-adaptive complex which evolved during the period of formation of tundra ecosystems. In this complex, one clearly sees the features of a self-regulating system (Fig. 16.98), the dynamics of which undergo significant modifications by abiotic factors.

Thus, we have considered in more or less detail only four components of the trophic levels of animals; the complexes of phytophages, saprophages, insectivorous birds, and predators eating the lemmings. These complexes were selected because they are better studied and more representative than others. Food relationships of predatory invertebrates have been poorly investigated so far, although this complex is very diverse in the tundra including several groups of mites (Gamasina, Bdellidae, and others), spiders of the families Lycosidae and Linyphiidae, predatory bugs (Saldidae), beetles (Carabidae, Dytiscidae, Staphylinidae), and many species of predatory dipterans, for example, *Rhamphomyia* (Empididae), Dolichopodidae, larvae of some Syrphidae, etc. Detailed study of the ecology of their cenotic role could contribute greatly to understanding the mechanisms of regulation of homeostasis in tundra ecosystems.

There are few data concerning the relationships between predators and birds. Extremely important for investigating the tundra phytocenoses would be data on microphytophagy – the feeding of animals on microalgae, fungi and bacteria. The complex of parasites was also not taken into consideration here, nor were cenotic relationships like symbiosis, commensalism, competition, etc., although many interesting works have been devoted to them. For example, the complex of insects which pollinate flowers has been under investigation for several decades in tundras of Canada and Siberia (see Chernov, 1966, 1978a). The mycorrhizae of tundra vegetation have also been rather well studied (Katenin, 1972). In recent years, the symbiotic relationships between procaryotic organisms and higher plants in the process of nitrogen fixation (Grunina and Getsen, 1984b; Getsen and Kostyaev, 1989) have been investigated. Many interesting data have been obtained on commensalism, symbiosis, and competition in vertebrate animals – for example, nests of "peaceful" birds next to nests of predators (Litvin et al., 1985) and competition between the predators of lemmings (Ovsyanikov and Menyushina, 1986). Nevertheless, even the limited data we have given in this brief review present evidence that, though there is a trend toward an increase in the role of abiotic factors in the formation of tundra ecosystems, these ecosystems are not completely dependent on climate. Complicated and rather efficient mechanisms of biocenotic regulation of population dynamics and ecosystems operate inside them. These mechanisms reflect on the one hand universal principles of synecological organization, and have on the other hand many particular features dependent mainly on two factors: the reduction in general biodiversity and the great rigor of the environment.

GENERAL TRENDS IN TRANSFORMATION OF THE ARCTIC ORGANIC WORLD AS A FUNCTION OF CLIMATIC FACTORS

Studies of life in the High Arctic latitudes present many vivid examples of the influence of progressively more unfavorable temperature conditions. Therefore, arctic landscapes represent the best model for establishing the general principles of ecology of extreme environments. The lack of heat in the tundra and polar desert does not often

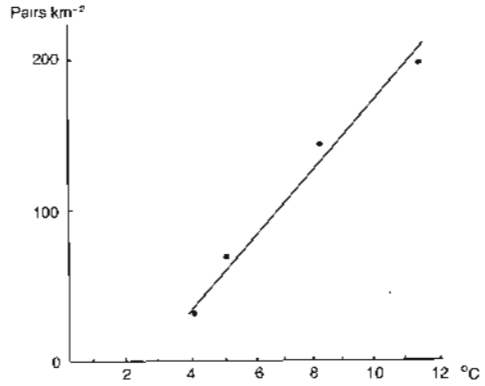


Fig. 16.99. Correlation between the density of bird nesting on "plakor" and the mean July temperature in Taymyr. Data of transect records recalculated to figures per unit area. Unpublished data of N. Vronskyi.

act directly, but through food sources, chemical properties of the environment, duration of activity, etc. Nevertheless, various parameters of life in the Arctic, in one way or another, are correlated with the temperature conditions, and for the understanding of general principles in the organization of communities and biota (taxa composition) in the Arctic concrete analyses of these relations are of great importance.

Here, we shall restrict ourselves to only one climatic index, namely, the mean temperature of the warmest month which in high northern latitudes, as a rule, is July. In spite of having some deficiencies, the mean July temperature is one of the most informative integrated indices of heat conditions for community formation in High Arctic latitudes (Chernov, 1978b, 1985; Chernov et al., 1983). The mean July temperatures for different arctic regions were obtained from three atlases (*Agroklimaticheskyi Atlas Mira*, 1972; *Atlas Okeanov*, 1980; *Atlas Arktiki*, 1985).

Various biotopic and synecological parameters, such as the number of species, biomass, and production, depend on the environment, on meso- and microclimate differences, and on the very diverse gradients within the landscape. When analyzing their correlations with climate, it is necessary to use certain principles. A selection of the elements of the living cover developing on "plakor" ("zonal" elements proper), which mostly correspond to climatic factors (Chernov, 1975), is one of the rules for these analyses. Figure 16.99 shows an example of a very strong correlation of the density of bird nesting in "plakor" conditions with the mean July temperature. The data are from a single region (Taymyr). It is natural that the dispersion will be greater if one uses data from different regions of the tundra zone (Fig. 16.100).

Figure 16.101 shows the relationship between the summer temperature over wide areas and the number of species in the local bird faunas. In spite of a high heterogeneity of data (numerous researchers often using different methods), the correlation with the temperature of the warmest month, especially within the tundra zone, seems to be very strong. This shows that general characteristics of tundra communities developing in "plakor" or similar environments are in strong correlation with air temperature. Obviously, in High Arctic landscapes where heat is the main limiting factor, this correlation is closer than in other, more favorable climatic conditions. It is clear that at lower latitudes, where air temperatures are higher, correlations become weaker.

On the whole, the richness of the local avifauna is positively correlated with the mean July temperature from the polar desert to the forest steppe. The number of species increases by 50–60 for every 10°C increase in July temperature. In High Arctic latitudes, such changes occur within one natural zone whose potential width is 500–600 km. Further south, however, similar changes cover three

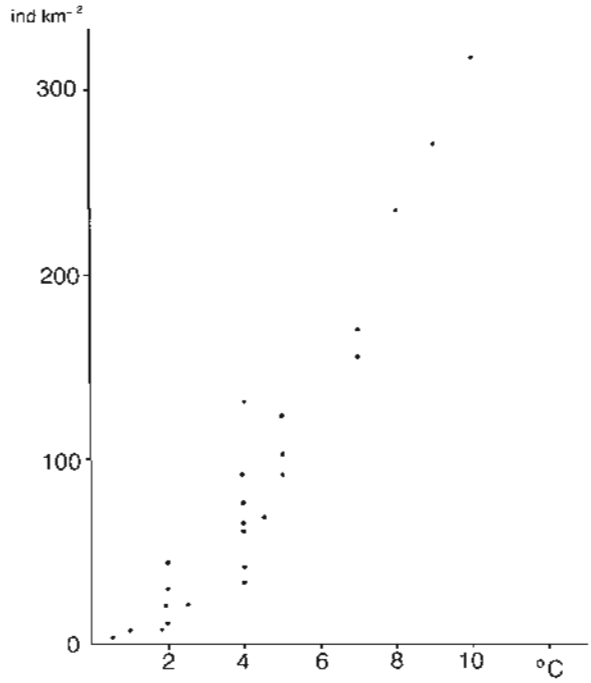


Fig. 16.100. Relationship between the density of bird populations per unit area (km²) on "plakor" in summer over the whole Arctic and mean July temperature. From Stishov et al. (1989).

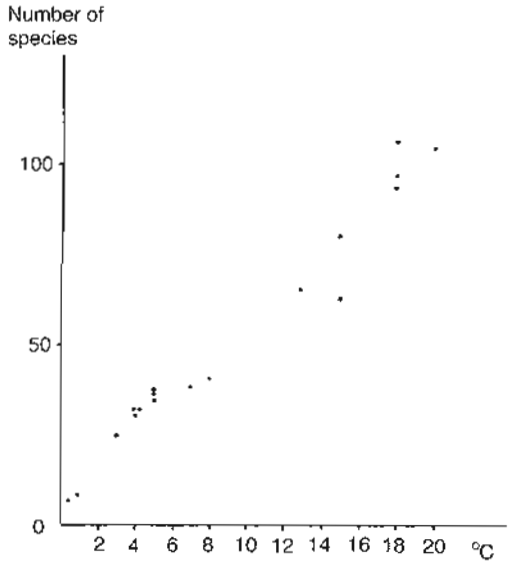


Fig. 16.101. Relationship between the species number of birds in local faunas in the middle Siberian sector and mean July temperature. From Chernov (1989).

zones, and over a distance four times as great. This example reflects a general regularity according to which the geographical environment and many parameters of communities and ecosystems change much more sharply in the Arctic than under more favorable conditions (Chernov, 1975, 1978b, 1985). However, it would be incorrect to think that the synecological organization of the tundra biome is absolutely exogenous – in particular, climatically determined. Its living cover still retains significant cenotic autonomy. For instance, in Taymyr a single ass. *Carici arctisibiricae–Hylocomietum alaskani* Matveyeva 1994 with the same dominants prevails over the entire tundra zone (Matveyeva, 1994).

Even in the Arctic, however, not all biological parameters are rigidly correlated with changes in temperature conditions. The biological peculiarities of species, such as their body size, mobility, specificity of the life cycle, distribution over biotope, etc., are able to modify these correlations. For instance, the number of Collembola species in local faunas from the polar desert to the deciduous forest is closely connected with summer temperatures (see Fig. 16.23 above). However, sets of species in particular communities corresponding to the most typical "zonal" associations have a very low "threshold of species saturation" (only about 35 species). This value is already reached in the typical tundra subzone, and further south, down to the deciduous forests, the number of species recorded in particular "zonal" communities hardly increases. Obviously, there is a certain limit of co-existence of species in cenoses which is determined by demographic factors.

An interesting example demonstrating the complexity and ambiguousness of the dependence of biota components on climatic factors is given in Figure 16.102. It reflects the correlation between the number of spiders in a local fauna and the mean July temperature. Open circles are data from Siberian regions (Yamal, Taymyr, Putorana plateau), solid circles from northeastern Asia and arctic North America, from Kolyma plateau (=Kolymskoe plato) to Ellesmere Island. In each of these groups of points, one can see an independent and very strong relationship between the number of species and temperature. Under

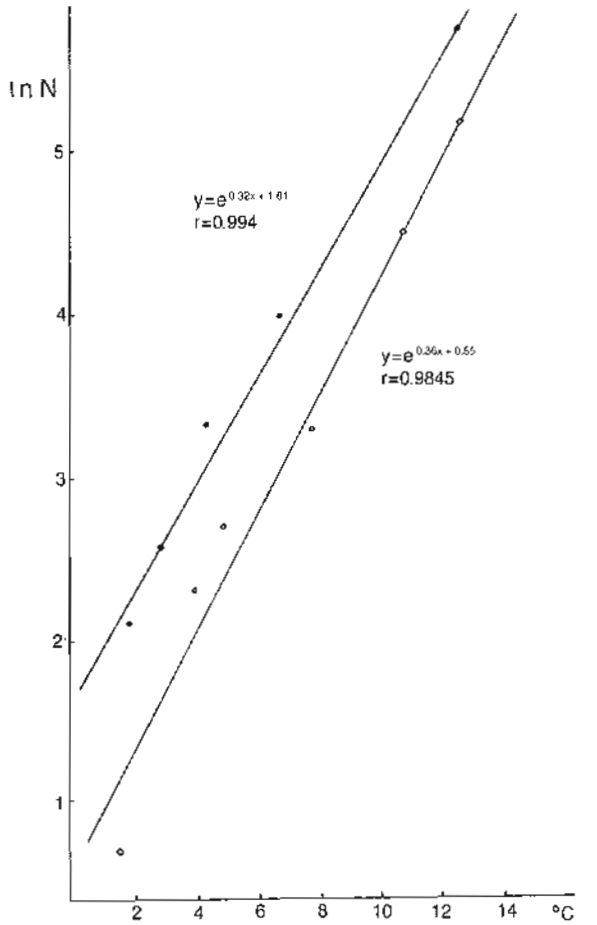


Fig. 16.102. Correlation of the natural logarithm of the number of spider species in local faunas with mean July temperature. Solid circles from American–Beringian regions; open ones from the Siberian sector. From Chernov (1989).

corresponding conditions of summer temperature, the number of species in the American–Beringian region is always higher than in middle Siberia. The higher species diversity in the Beringian sector of the Arctic is mirrored in other groups of organisms. Thus, the vascular plant flora (Petrovskyi, 1973) and entomofauna (Berman, 1986) of Vrangel Island are very rich in comparison with the analogous landscapes of middle Siberia.

Several probable explanations for these correlations can be postulated: (1) different reactions to temperature conditions (that is, differing optimal temperature) for species of comparable faunas and floras formed in different palaeoclimatic conditions; (2) different age: in the very old Beringian biota, a large number of species had time to evolve; and (3) differences in the real temperature conditions in local environments with similar macroclimatic parameters. The last explanation, perhaps, is the most prosaic and least attractive for biogeographers, but it is the most suitable to ecological common sense. If one compares isotherms in the Arctic, it is easy to see that summer temperatures are essentially different at the same latitudes of different comparable sectors. In Siberia at 70°N the mean July temperature usually varies between 10 and 12°C, while in northeastern Asia and in North America at the same latitude it is about 6–8°C and in places even 2°C. On the Chukchi peninsula (Chukotskyi Poluostrov) at the Arctic Circle, the mean July temperature is about 6–8°C. This is the reason why analogous types of landscapes in the Siberian and North American sectors are situated at very different latitudes. For example, in Taymyr the arctic–tundra subzone occurs mainly north of 74–75°N, while Vrangel Island with its arctic tundra is situated at 71°N. In the North American sector, arctic tundra even reaches as far south as 65°N (Aleksandrova, 1977). In any case, the temperature of the warmest month in the arctic–tundra subzone, independent of the latitude, is about 3–5°C. Naturally, in the more southerly latitudes with similar summer temperature conditions, some elements of the radiation balance can be higher (see Fig. 16.4 above). Thus, in arctic North America in comparison with the corresponding latitudes in Siberia, the summer is colder, but the duration of sunshine and the total radiation are higher (*Atlas Arktiki*, 1985). Temperature conditions in elements of the relief, compared to analogous types of "zonal" communities, can vary greatly because of the variation in radiation. Thus,

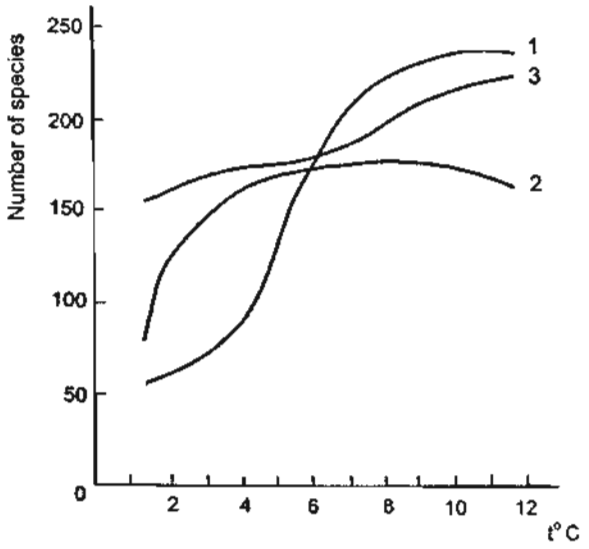


Fig. 16.103. Species richness in the local floras on Taymyr in relation to mean July temperature. 1, vascular plants; 2, mosses; 3, lichens.

for Vrangel Island the mean July temperature is accepted to be 3°C, which probably corresponds to the seashore. In central parts of the island, however, in valleys between mountains, the mean July temperature can reach 10°C (Svatkov, 1970), the same values measured at the same latitudes in Taymyr. Distinctions like this in the real temperature conditions can lead to essential distinctions in the biotic composition in analogous landscapes situated in sectors with different degrees of continentality. In particular, the "intrazonal" communities can be quite different in spite of the great similarity of "zonal" vegetation. A longer duration of bright sun can promote better soil heating, which is of great significance for the life of soil invertebrates and microorganisms.

Undoubtedly, in some cases nonclimatic factors can even be of major significance for the biology of arctic regions, for instance the evolution of floras and faunas. Thus, Yurtsev (1986) postulated that the main reason for the high richness of vascular plants in the flora of Vrangel Island is its great age and special factors in the evolution of its flora. It is necessary, however, to notice that historical factors cannot radically change all the quantitative correlations of species richness with temperature which are primarily responsible for the ecological potentiality of environments. Historical factors act only within the limits of these general correlations.

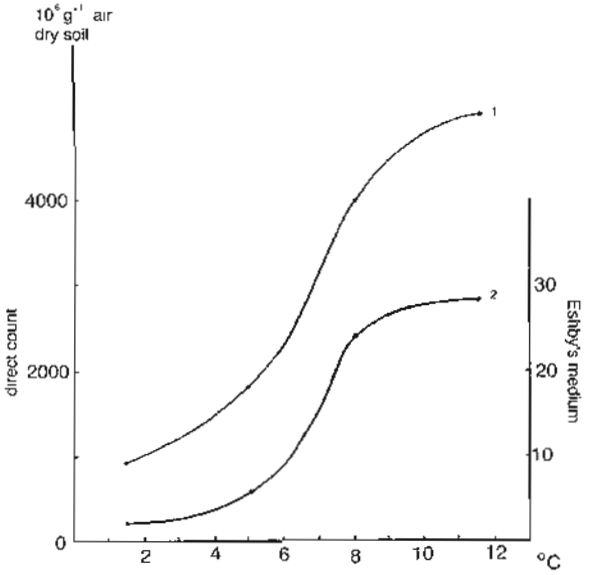


Fig. 16.104. Relationships between bacterial numbers in soil and mean July temperature in "zonal" communities in Taymyr. 1, direct count; 2, Eshby's medium. From Parinkina (1989).

The dependence of the distribution of a taxon on climatic factors is affected, among other things, by the evolutionary level of the taxon (Chernov, 1988). Figure 16.103 shows the relationship of the number of species of three plant groups changes in summer temperature from southern tundra to polar desert. This figure illustrates well the greater adaptive possibilities of more primitive groups (mosses and lichens) in comparison with more advanced types (vascular plants) in the cold landscapes of the highest latitudes.

The correlation of parameters of the community structure and biota with the climatic temperature gradient is not always direct. Using ordinary, nonlogarithmic scales, these correlations are often described by similar S-shape curves which, in general, reflect a logistic dependency with an exponential growth (Figs. 16.104–16.107). Similar types of curves describe animal growth and the increase in population numbers. In a given case, such curves have been obtained for changes in both quantitative synecological parameters and the richness of floras and faunas.

The sharpest increase in various biological parameters is observed between mean July temperatures of 4° and 8°C – that is, from the middle part of the arctic tundra to the southern part of the typical tundra subzone. The increase in these parameters slows down above 8°C. This flatter part of the curve usually corresponds with the southern tundra subzone or the forest tundra, where the limiting role of summer temperatures is not as great as at higher latitudes. There is also a zone on the curves which corresponds with the polar deserts and the northernmost variants of the arctic tundra (with 3–4°C as the mean July temperature), where an addition of 1–2°C does not essentially change the general lack of heat.

As mentioned above, the global relationship between biotic parameters and summer temperatures is quite linear. However, various parts of these general features can have, in principle, different characters. In this connection, an interesting example is, given by birds. Figure 16.101 above shows generally linear relationship between the number of species in local avifaunas and the mean July temperature over larger areas, while, at lower temperatures, an S-shaped relationship can be detected. Tundra data, not only for a single geographical sector, but for the entire Russian Arctic, are shown in Figure 16.105. Despite an increase in general dispersion, a typical S-shape curve may be seen here. It is still impossible to fully explain this phenomenon. It may be supposed that, by the use of better data, one may find logistic correlations at different levels of the temperature gradient. In other words, there may be transition areas due to changes of species complexes in particular temper-

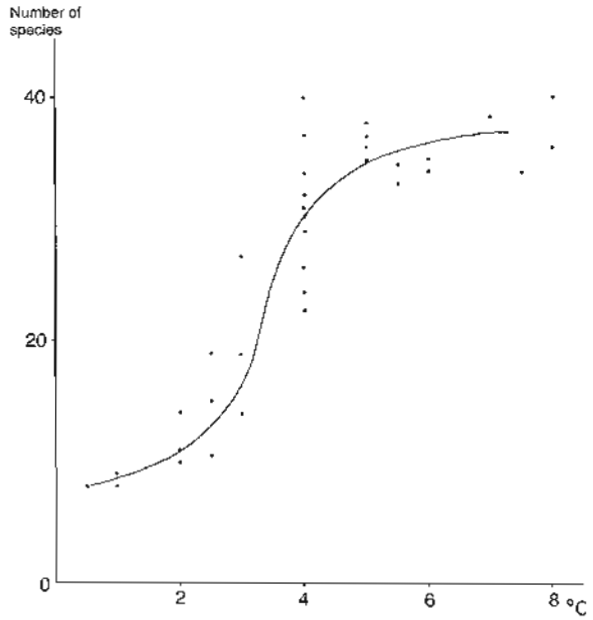


Fig. 16.105. Relationships between the number of species of birds in local faunas over the whole Arctic and mean July temperature. From Stishov et al. (1989).

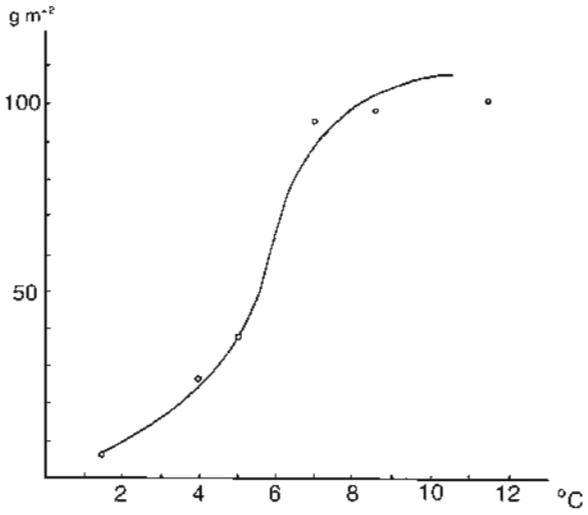


Fig. 16.106. Annual aboveground productivity of vascular plants in "zonal" communities in different tundra subzones and polar desert related to mean July temperatures in Taymyr. From Chernov et al. (1983).

ature ranges. This could perhaps be explained by the discrepancy already mentioned between the temperature gradient and the changes in general landscape organization.

A probable artifact exists through the use of the same temperature parameter (the mean July air temperature) at different latitudes in various zones. Obviously, the shorter the summer, the more the mean temperature of the warmest month will reflect general heat conditions. Correlations of the biota and communities with climatic factors may be better expressed if different temperature parameters are used in different parts of the global gradient.

Figure 16.106 shows another typical example of a logistic relationship within the tundra zone. It reflects the change in total aboveground production of vascular plants in the *Dryas punctata–Carex ensifolia* ssp. *arctisibirica–Hylocomium alaskanum* frost-boil "zonal" community of the Taymyr. In this case, the primary production was calculated for the entire community area, taking into account the ratio of different elements (rims, troughs, and patches of bare ground) with quite diverse values of primary production (Chernov et al., 1983). The most productive element of this complex is the vegetation at the convex rim, which is warmest and moderately dry. Against the background of the considerable change in the total primary production of all structural elements of frost-boil tundras, the values of primary production on the rims is strikingly consistent, from the southern tundra subzone up to the southern part of the arctic tundra subzone, about 150 g m^{-2}. In the arctic tundra subzone, this element of community structure disappears, which leads to a sharp reduction in the whole productivity, almost to half. The plant cover on the rim is formed mainly by *Carex ensifolia* ssp. *arctisibirica*, which is the main component of the terminal stage of succession in "zonal" vegetation on "plakor" in Taymyr. Therefore, in this case an essential decrease in the general primary production of the community is due to the lack of one species, which is the most productive. This reflects one of the main principles of organization of communities and biota as a whole, called the "block principle" (see Chernov, 1984a). Thus, studying the dependence of changes in total synecological and biotic parameters on climatic factors, one must keep in mind that the separate structural elements of a given system can show quite different correlations.

A comparison of responses to the climatic gradient of "zonal" and "intrazonal" elements of cover, which can be considered as blocks of single landscape systems, might be very interesting. As mentioned above, the parameters of "zonal" communities developing on "plakor" are most rigidly correlated with climatic gradients. This was well illustrated by data on nesting density of birds and on aboveground production of vascular plants.

As is seen in Figure 16.106, the aboveground plant production of Taymyr "zonal" tundra communities increases by a factor ten from the polar desert to the southern tundra. Variations in production of diverse "intrazonal" communities such as mires, marshes, and some grass–forb meadows are far less dependent on macroclimate. The distinctions in productivity between local variants of closely related community types cannot be less important than between communities from different subzones. Naturally, if very closely related types from different subzones are studied, it is possible to obtain a rather clear gradient in production. Thus, an analysis of grass–forb meadows of similar biotopes on southern slopes of river banks in different subzones gives the values shown in Table 16.39.

However, if one takes different meadows from each of these sites, the values of their productivity will vary over a wide spectrum. Thus, in Dikson (southern part of the arctic tundra subzone), some

TABLE 16.39

Maximum vascular plant production of grass–forb meadows in different subzones on Taymyr[1]

Subzone	Site	Mean July temperature (°C)	Aboveground production (g m^{-2}) (air-dried, general maxima)
Arctic tundra, northern part	Maria Pronchishcheva Bay	+ 4	71.5
Arctic tundra, southern part	Dikson	+ 5	146.4
Typical tundra, northern part	80 km south of Dikson	+ 7	194.0
Southern tundra	Kresty	+12	220.0

[1] From Chernov et al. (1983)

meadow types show an aboveground primary production of about 50–70 g m^{-2}, close to the general values for meadows from the northern parts of arctic tundras. In the northern part of the typical tundra subzone (80 km south of Dikson) in very peculiar meadows with *Allium schoenoprasum*, *Cortusa matthioli*, *Hedysarum arcticum*, and *Sanguisorba officinalis*, this value reaches 311.5 g m^{-2}. This is larger than the maximum values obtained for natural meadows from the southern tundra subzone (Kresty), where the majority of meadow communities show a value less than 200 g m^{-2} (148.8; 158.0; 189.6) and the maximum value obtained was 220 g m^{-2}. The maximum values of aboveground plant production of anthropogenic meadows (which can also be considered as "intrazonal") of various subzones are very similar. In the arctic tundra subzone it is 472 g m^{-2} and in the southern tundra subzone 448 g m^{-2} (Chernov et al., 1983).

All these data reflect a general regularity. Rigid "zonal" correlations of biological parameters with climate are typical for "plakor" elements of landscapes. In the "intrazonal" environments where climatic gradients, are smoother, the corresponding communities are usually more similar to each other over a very wide spectrum of landscape "zonal" conditions.

The role of "intrazonal" landscape elements in smoothing out climatic severity is well illustrated by the distribution of species numbers in different taxonomic groups. It is natural that in extreme climatic conditions, such as the polar desert and the tundra, a relatively large number of species are connected with special local biotopes (lake shores, south-facing slopes, etc.). Thus, in the tundra zone about half the species in many groups of organisms – for example, dicotyledons, insects, soil beetles, mites, etc. (Table 16.40) – occur in grass–forb meadows, which occupy a very insignificant area compared with "plakor" environments.

Progressing northward, the proportion of species inhabiting "plakor" biotopes becomes greater, which can be clearly seen, for instance, in birds from different regions of the Russian Arctic (Table 16.41). In Taymyr, in the typical tundra subzone, only 20–33% of birds live in "plakor" environments. This demonstrates the high significance of "intrazonal" parts of the landscape in the life of birds. In the arctic tundra subzone, the proportion of bird species nesting in "zonal" communities proper increases to 48–50% (Chernov, 1978b;

TABLE 16.40

Number of species of soil invertebrates in various types of communities near Tareya, Taymyr[1]

Group	Total number of species in the local fauna	Percent of local fauna			
		Frost-boil tundra with 20% bare ground	Hummocky tundra with closed cover	Polygonal mire	Herb meadows on southern slopes
Nematoda	162	50.6	23.5	17.9	51.9
Oribatei	33	36.4	39.4	33.3	45.5
Collembola	62	53.2	43.5	35.5	61.3

[1] From Chernov (1978b).

Vronskyi, 1986). The same regularities are recorded for vascular plants (Matveyeva, 1979b). Therefore, the proportion of species inhabiting "plakor" increases as temperature conditions become more adverse. In the polar deserts, the majority of "intrazonal" communities, such as meadows and mires, are absent. This is explained by the lack of heat which, at the highest latitudes, becomes a universal controlling negative factor, so that neither exposure, moisture, nor any other factor can ameliorate the prevailing climatic harshness.

Figure 16.107 demonstrates one more important mechanism for transformation of biota depending on a climatic gradient. It also describes a positive correlation between the species diversity of local floras and the mean July temperature. Changes in species number in the entire vascular plant flora are described by an S-curve, as in the examples given above; but it is also very interesting that each plant family shows its own specific curve form. It is clearly seen that a northward decrease in species diversity does not occur in all families. There is a well-defined tendency toward an increase in the number of species in Brassicaceae and especially in Saxifragaceae in the arctic tundra subzone, and this level is maintained even in the polar desert. This shows indirectly that in this case one can consider the entire flora as a very rigidly organized system with families as the elements. One is faced here with the landscape analogue of the individualistic principle of changes in community composition forming the basis of a spatial continuum (Ramenskyi, 1938). This shows that the individualistic principle can be useful both above the species level and on the landscape–zonal scale. It can be accepted, perhaps, that the continuum manifests itself very differently from the local cenosis up to the "zonal" scale.

TABLE 16.41

Proportion of birds inhabiting "zonal" communities proper in the Russian Arctic. Mean data of different regions[1]

Subzone	Number of species in local fauna (A)	Number of species in "zonal" communities (B)	B/A
Arctic tundra			
Northern part (8 sites)	15.8	8.0	0.52
Southern part (5 sites)	35.6	15.8	0.45
Typical tundra	38.0	16.2	0.43

[1] From Stishov et al. (1989).

CONCLUSIONS

The data discussed in this chapter allows one to summarize some general organizational features of the tundra biome.

Proceeding north within the tundra zone one sees:

(1) an increasing impoverishment in the taxonomic composition, though these changes are uneven. Along with the general lowering of diversity, there are certain taxa which all demonstrate common signs of biological progress in the Arctic.

(2) There is a relatively large proportion of phylogenetically primitive taxa. This leads to a predominance of adaptive strategies of a passive type.

(3) In comparison with other biomes, there is a stronger positive correlation of the main parameters of tundra communities and ecosystems with various temperature conditions.

(4) There seems to be a compensation for the generally lower taxonomic richness and ecological diversity by a relatively high concentration of species in particular communities, by a widening of ecological amplitudes and niches, and by an increased population density of certain species.

(5) There is a decrease in production along with an increase in accumulation of organic matter. This means an increase in the ratio of biomass to production and as a consequence a generally low rehabilitation potential.

(6) Reduced succession rates with an increase of pioneer, permanently pioneer, and successionally young communities are characteristic of the living tundra cover.

(7) The communities generally lack autonomy and are responsive to the environment rather than transforming it.

(8) The communities tend to show well-pronounced diverse geometrical forms and a high regularity, reflecting their dependence on physical factors of the environment.

(9) The interrelations between organisms and biotic and abiotic environments are imperfectly regulated. On the other hand, certain functional links and co-adaptive complexes are strictly regulated by complicated cenotic mechanisms.

The tundra biome is situated at the margin of

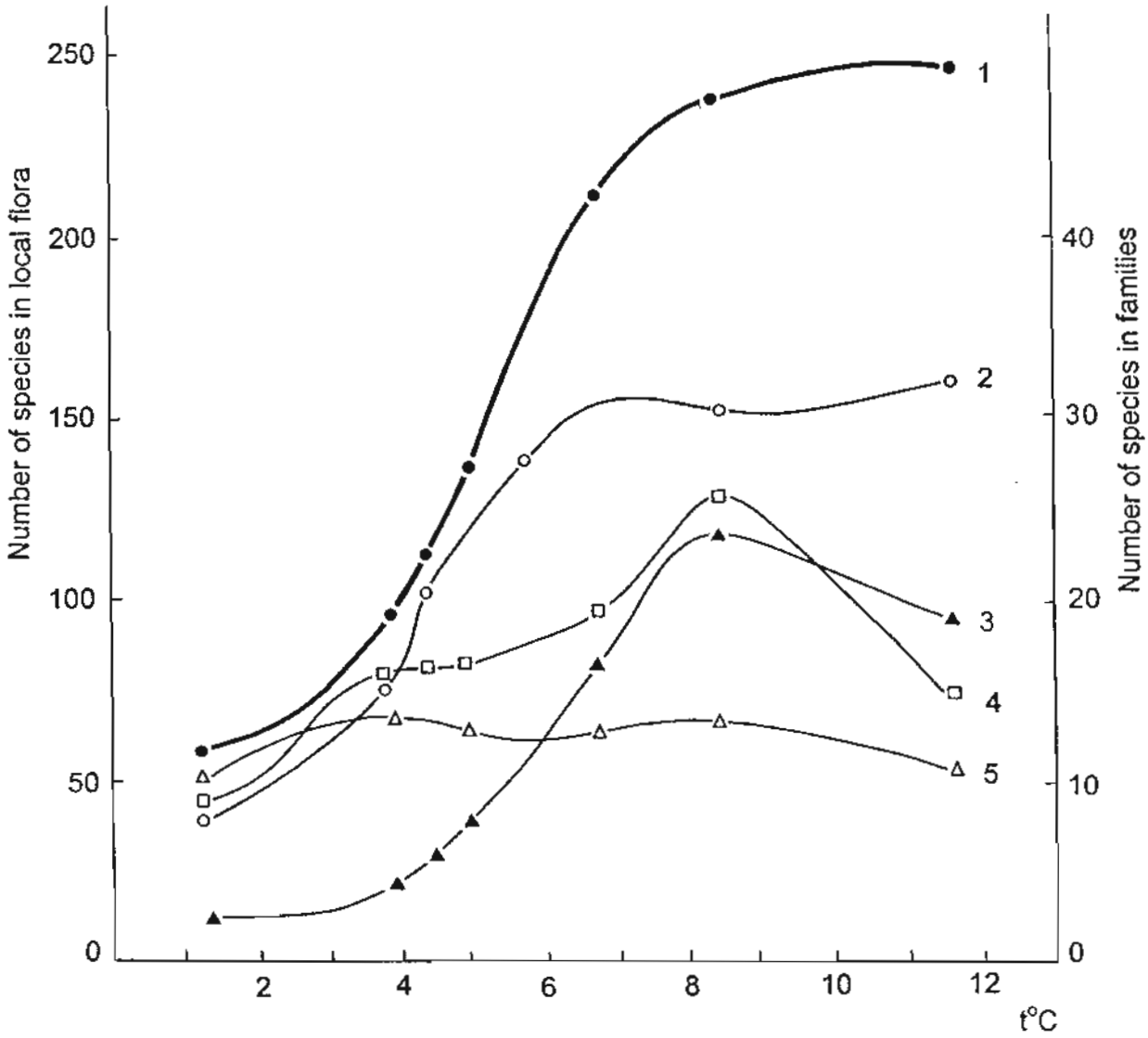


Fig. 16.107 Species number of vascular plants in certain plant families in local floras on Taymyr related to mean July temperature. 1, the whole flora; 2, Poaceae; 3, Cyperaceae; 4, Brassicaceae; 5, Saxifragaceae. From Chernov (1989).

the global spectrum of climatic conditions, at the limit of existence of life on earth. This determines the main peculiarities of the organization of communities and ecosystems of this zone. Many characteristics of the communities, such as taxonomic richness, biomass, and production, are much lower than in southern biomes. They decrease dramatically in the humid belt from the forest steppe and deciduous forests towards the tundras and further north to the polar deserts (Chernov, 1975).

All this, however, is true only in a generalized, summary sense (when one speaks about the ecosystem as a whole). In the tundra biome, numerous mechanisms are operating which partly compensate for the negative changes in communities and thus contribute to the preservation of complex forms of cenotic organization. One example is the non-uniformity in the decrease of taxonomic and ecological diversity. In spite of the general decrease in the number of taxa at increasing latitude, some particular taxa increase their relative, and sometimes their absolute, significance in the high-latitude landscapes. This leads to a conservation in the tundra of many forms of organization of communities and cenotic relations, and even to an increase in the complexity of some of them. A good exam-

ple is given by the suborder Charadrii as a whole, and especially by sandpipers (*Calidris*). This is one of the few examples of wide adaptive radiation at high latitudes. In *Calidris* particularly, very complex inter- and intraspecific relations are developed in the tundra, whose analogs are hardly to be found in the boreal avifauna. Instead, they resemble situations observed among tropical birds. This is manifested in both the extreme complexity of reproductive processes and the diversity of trophic niches, morphology, coloring, and the complex structure of the population. In the world of plants, similar examples are given by *Draba*, *Pedicularis*, and especially *Saxifraga*.

Various sections of this chapter have also been devoted to other mechanisms of compensation for the decrease in taxonomic diversity: the phenomenon of superdominance which is a result of widening ecological niches for a decreased number of species, formation of various plant and animal communities by reshuffling a small group of species common to all of them; a relative richness of local floras and faunas; a very high concentration of species in area unit of a community (it happens that, in an area of a particular tundra phytocenosis, there are more species than in the forests and even in the steppes).

Especially clearly pronounced is the ecological integrity of taxa at the northern limit of the tundra biome. Many of them are represented by solitary species which, however, continue to perform essential and diverse ecological functions characteristic of the taxon as a whole. A great role is played by ecological plasticity of the species. All this leads to the possibility of the formation of various relatively complicated cenotic groupings conforming with the variegated spectrum of abiotic conditions.

The organisms and communities in the arctic landscape are to a large degree subject to the direct adverse effect of abiotic factors, primarily by the lack of heat and its consequences (shortness of the growing season, lack of nitrogen, etc.), with a decrease in the role of cenotic factors. However, despite the simplification of the general functional and cenotic organization of the tundra communities, they should not be considered exogenous, fully dependent on climate. In the ecosystems at high latitudes, complex regulatory feedback mechanisms are still well developed. This refers primarily to the organization of trophic chains and networks. There is no question that the limiting and regulating role of food is increased in severe arctic conditions. Food shortages arise here more frequently as a result of the concentration of main food links around a small number of objects caused by the reduction in secondary and substitute food sources. All this tends to create quite peculiar relations in the trophic system of tundra ecosystems. Competitive relations in the tundra cenoses are also special, but have not yet been sufficiently studied. The principle of competitive exclusion, in particular, appears to be clearly manifested here.

The very high level and complexity of cenotic organization are also shown by the relative stability of some syntaxa, which retain their constancy of composition within wide ranges of environment. One example is the *Carici arctisibiricae–Hylocomietum alaskani* Matveyeva (1994) developed in the Taymyr from the southern to the arctic tundras.

The cardinal distinction of tundra communities from those of the forest are indisputable. Together with this, both within the Subarctic and the Arctic, the continuum of communities is very strongly pronounced. The synecological organization changes markedly; moreover, the changes of many parameters within the tundra zone are more fundamental than at its border with the forest belt. An especially marked transformation is undergone by biocenoses in the northern half of the tundra zone, on the borderline between the typical and the arctic tundra. This is determined by sharp gradients in temperatures and by the great ecological importance of heat under these severe conditions. All this indicates that the borderlines made by man are purely conventional and that the synecological organization of the living cover is continuous.

The tundra biome, as well as the polar desert, is unique in its dependence on a single factor, temperature. This is reflected by the rigid correlation of various parameters of ecosystems and the composition of flora and fauna with summer temperature conditions. These dependencies, as a rule, are of a typical logistic character with a more or less distinct zone of exponential increase. In this sense, the organic world of the tundra may serve as an excellent model for the elucidation of general regularities of the effect of factors on various forms of life.

Numerous peculiarities have been shown by studies of the temporal transformation of ecosystems at high latitudes. In particular, the tundra communities are most specific in their succession

processes. These successional series are shortened in the tundra zone and there is a very high proportion of pioneer, or more exactly permanently pioneer, communities. This especially refers to the very diverse stands on bare ground arising in various ways.

The tundra and, especially, the polar desert cenoses show phycocenogenic primitivity. This is observed in the predominance of many primitive groups of organisms — for example, the dominance (which increases towards the higher latitudes) of mosses, lichens and algae, with a distinct loss of the leading position of vascular plants, in particular of dicotyledons, in the phytocenoses. In high latitudes, vascular plants do not form a full phytocenosis without participation of mosses and lichens. Vascular plants are typical for various disturbed ecotopes, forming incomplete pioneer communities and taking part in the processes of primary succession. In the subsequent stages of succession, however, they often give way to cryptogams.

The signs of biological progress of primitive archaic taxa and their comparatively large share in communities in tundra landscapes are due to adaptational, historical, and biogeographical reasons. In particular, there are reasons to believe that the more primitive evolutionary forms are apt to show passive adaptations and have a high tolerance, which is especially valuable under severe abiotic conditions.

Hydrophilous communities (especially of animals) are varied and important in the tundra zone. On the northern tundra border, and especially in polar deserts where the formation of hydrophilous communities is difficult and pools become more and more lifeless, the number of true hydrobionts is reduced. In terrestrial biotopes in polar desert, however, primary or secondary hydrophilous forms or their close relatives are predominant. The main food chains are based not on macrophytes, but on algae. In other words, a kind of transposition of the water ecosystems onto the land takes place (Matveyeva and Chernov, 1976; Chernov et al., 1977, 1979), again emphasizing the primitive character of synecological organization.

Thus, the pioneer character and curtailment of succession at high latitudes are combined with a phycocenogenic primitivity. The analogy can be drawn with the law of ontogenesis: successionally young stages correspond with early stages in the evolutionary development of communities. From this point of view, tundra and polar desert communities are highly interesting as models for establishing some fundamental general biological regularities.

Data on the internal structure of communities are important in understanding their synecological organization. The species structure, or species diversity, of communities at high latitudes is most peculiar. The general decrease in floristic and faunistic diversity is partly compensated by an increased concentration of species in small areas of particular communities. Many structural and functional elements of tundra communities, however, have a very simple structure. They are formed by a few (or only one) species. Another consequence of a low taxonomic richness is an increase in density. However, high population density of certain species is associated with low productivity or with strong fluctuations, instability, or poor resilience. A great population density of certain species is not a result of high production. It is rather accumulation and conservation than productivity. This is just the reason why rich populations of game animals in the North are so quickly reduced or completely destroyed.

Low productivity combined with poor diversity is one of the main causes of fragility and low stability of the tundra ecosystems, in which the possibilities for renewal or modification are low. Yet, at the same time, an important role is played here by plastic eurytopic species, the superdominants, which participate in various cenotic combinations. Such species are, however, few, and strong fluctuations in some of them may lead to catastrophic consequences for the ecosystems.

Lability and resistance are more characteristic of the adaptive strategies of tundra organisms than are mobility and active survival. This may give an effect of false stability of the ecosystems.

Unfortunately, the internal structure of tundra communities has been very poorly studied. Meanwhile, the few data available could provide a lot of fundamentally new knowledge for the general theory of stability and steadiness of ecosystems, because it is just under extreme conditions that some forms of synecological organization and the mechanisms for its regulation will be most clearly manifested.

Beta-diversity, or differentiation in groupings of organisms depending on the gradients of the environment, is less in the tundra than in more southerly biomes. The number of plant associations is

low and stratification is reduced in both the vegetation and the invertebrate communities. However, due to the decrease in the activity and autonomy and the increase in external control, tundra communities have a very complicated spatial structure. The pattern of the vegetation cover is highly ordered. This is especially true of the mosaic and regular-cyclic types of structures clearly seen in the geometry of patterned ground. On the one hand, this can be interpreted as primitiveness in the morphology of communities as a result of their weak ability to influence the environment. On the other hand, they show certain stability, which is due to the low speed of successional processes.

Tundra communities, vegetation, and animal populations are more dependent on the relief than are more southerly biomes. In tundra, as in no other zones, a very great role is played by the nanorelief. The nanorelief determines the elementary constituent parts (synusia, microgroupings) of the cover mosaic. The microrelief determines non-uniformity at the association level, while the mesorelief differentiates the cover into "zonal" and "intrazonal" (including "extrazonal") elements. The complicated regularities of distribution of communities over the landscape profile are determined by the interrelation of all these elements.

In arctic conditions, an especially important role is played by the smoothing of climatic gradients which occurs in the "intrazonal" parts of the landscape. This is the reason why many groups of organisms and types of communities overcome the sharp climatic boundaries of high latitudes. The tundra biota is enriched with representatives of southern floras and faunas which increase the syntaxonomic diversity and general differentiation of the living cover. It is just in the "intrazonal" communities that production in the arctic climate is the highest. In some cases, similar effects are the result of anthropogenic influence leading to the formation of highly productive communities differing markedly from those of the natural tundra, also to be grouped with the "intrazonal" communities.

The macrostructure of the living cover of the arctic landscape on the geographical scale is also of a peculiar character. First and foremost is the separation of subzones and the drastic changes of many parameters (productivity, diversity, abundance) from the forest tundra up to the polar desert. These changes are so great, that averaged values for the communities and ecosystems over the tundra zone as a whole are of little value. It follows that no general estimates should be applied in working out economic measures. As nowhere else, the tundra zone requires a differential approach to the utilization of its resources.

The most essential peculiarities of tundra ecosystems are determined by the interrelations between the plant cover and the permafrost. The dynamics of the thawing of the permafrost and the thermal conditions of soils depend on the degree of development of the moss turf. Powerful modifying factors are the nano- and microrelief and the exposure of the slopes. An important role in these processes is played by animals: for example, lemmings which periodically destroy the moss cover over considerable areas or else the earthworms which loosen the soil and promote the growth of grasses, antagonists of mosses.

An important aspect of tundra synecology is the interrelation between herbaceous plants and mosses. Grasses and forbs are most active in areas devoid of moss cover (on bare ground in polygonal arctic communities, on eroded slopes and landslides, along sandy or muddy banks of rivers and lakes). In the tundra zone, the most productive grass communities are formed on areas without moss cover. The highest primary production is seen in meadows on south-facing slopes, where most favorable thermal conditions in the soil are maintained and the permafrost is at maximum depth. It is often sufficient that a slight stimulus should occur, such as destruction of the moss cover, in order that dynamic highly productive meadows appear in the place of poorly productive tundra communities. This forms the basis of the idea of increasing biological productivity of tundra areas by creating meadow communities in place of artificially eroded moss tundras (grass establishment on the tundras). So far, however, the tundra essentially remains the only natural zone with practically no agriculture, no agrocenoses.

The herb–grass meadows in the tundra zone are "intrazonal" communities which correspond, not to the general climate, but to local optimal conditions. The chief parameters of these communities are sharply different from those of the real tundra. In mossy tundra, the biological turnover of substances takes place in the thin moss-peat layer where the annual increment and death of the aboveground resources are insignificant. In the meadow system, the soil annually receives almost

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.

REFERENCES

Abramova, A.L., Savich-Lyubitskaya, L.I. and Smirnova, N.Z., 1961. *Opredelitel listostebelnykh mkhov Arktiki (Handbook of Arctic Mosses)*. Izd. AN SSSR, Moskva-Leningrad, 714 pp.

Afonina, O.M., 1978. Flora listostebelnykh mkhov (Moss flora). In: B.N. Norin (Editor), *Ary-Mas. Prirodnye usloviya, flora i ratitelnost*. Nauka, Leningrad, pp. 87–97.

Agroklimaticheskyi atlas mira (World Agroclimatic Atlas), 1972. Gidrometeoizdat, Moskva-Leningrad, 115 pp.

Alekhin, V.V., 1951. *Rastitelnost SSSR v osnovnykh zonakh (Vegetation of the USSR Main Zones)* (in Russian, with English summary). Sovetskaya nauka, Moskva, 512 pp.

Aleksandrova, V.D., 1956. Rastitelnost yuzhnogo ostrova Novoi Zemli mezhdu 70°76′ i 72°12′ N (Vegetation of Novaya Zemlya island between 70°56′ and 72°12′ N). In: B.A. Tikhomirov (Editor), *Rastitelnost Krainego Severa i ee osvoenie*, 2. Izd. AN SSSR, Moskva-Leningrad, pp. 188–306.

Aleksandrova, V.D., 1959. (Review). E. Churchill and H. Hansen. The concept of climax in arctic and alpine vegetation. The Botanical Rev. 24(2–3): 127–191. *Bot. Zh.*, 44(7): 1018–1023.

Aleksandrova, V.D., 1960. Fenologiya rastenyi i sezonnye aspekty v podzone arkticheskikh tundr (Plant phenology and seasonal aspects in the arctic tundra subzone). In: E.N. Sinskaya (Editor), *Trudy fenologicheskogo soveshchaniya*. Leningrad, pp. 209–218.

Aleksandrova, V.D., 1961a. Sezonnaya dinamika rastitelnykh soobshchestv v Arktike (Seasonal dynamics of plant communities in Arctic). *Probl. Severa*, 4. Moskva-Leningrad, pp. 60–74.

Aleksandrova, V.D., 1961b. Vliyanie snezhnogo pokrova na rastitelnost v arkticheskoi tundre Yakutii (Influence of snow cover in Yakutian arctic tundra). In: V.B. Kuvaev (Editor), *Materialy po rastitelnosti Yakutii*. Leningrad, pp. 190–221.

Aleksandrova, V.D., 1963. Ocherk flory i rastitelnosti o.Bolshogo Lyakhovskogo (An outline of flora and vegetation of Bolshoi Lyakhovskyi island). In: G.L. Rutilevskyi and R.K. Sisko (Editors), *Novosibirskie ostrova*. Morskoi transport, Leningrad, pp. 6–36.

Aleksandrova, V.D., 1970. Dinamika mosaichnosti rastitelnykh soobshchestv pyatnistykh tundr v arkticheskoi Yakutii (Mosaic dynamics of frost-boil plant communities in Arctic Yacutia). In: P.D. Yaroshenko (Editor), *Mozaichnost rastitelnyk soobshchestv i ee dinamika*. Vladimir, pp. 5–33.

Aleksandrova, V.D., 1971. Printsipy zonalnogo deleniya rastitelnosti Arktiki (Principles of zonal division of Arctic vegetation) (in Russian, with English summary). *Bot. Zh.*, 56,1: 3–21.

Aleksandrova, V.D., 1977. *Geobotanicheskoe raionirovanie Arktiki i Antarktiki (The Arctic and Antarctic: their Division into Geobotanical Areas)*. Nauka, Leningrad, 187 pp. (See also in English: Aleksandrova, V.D., 1980. *The Arctic and Antarctic: their Division into Geobotanical Areas*. Cambridge University Press).

Aleksandrova, V.D., 1983. *Rastitelnost polyarnykh pustyn SSSR (Polar Desert Vegetation of the USSR)*. Nauka, Leningrad, 141 pp.

Aleksandrova, V.D. and Zhadrinskaya, N.G., 1963. Smena aspektov v tundrakh ostrova Bolshogo Lyakhovskogo (Aspect changes in tundras of Bolshoi Lyakhovskyi Island). In: G.L. Rutilevskyi and R.K. Sisko (Editors), *Novosibirskie ostrova*. Morskoi transport, pp. 37–53.

Ananjeva, S.I., 1973. Nogokhvostki (Collembola) Zapadnogo Taimyra. (Springtails (Collembola) of Western Taymyr). In: B.A. Tikhomirov (Editor), *Biogeotsenozy taimyrskoi tundry i ikh produktivnost, 2*. Nauka, Leningrad, pp. 152–165.

Ananjeva, S.I. and Chernov, Yu.I., 1979. Nogokhostki (Collembola) v podzone arkticheskikh tundr na severo-vostoke Taimyra (Springtails (Collembola) in the arctic tundra subzone on the north-east Taymyr). In: V.D. Aleksandrova and N.V. Matveyeva (Editors), *Arkticheskie tundry i polyarnye pustyni Taimyra*. Nauka, Leningrad, pp. 148–153.

Ananjeva, S.I., Krivoluzkyi, D.A. and Chernov, Yu.I., 1973. Pantsirnye kleshchi (Oribatei) podzony tipichnykh tundr zapadnogo Taimyra (Beetle mites (Oribatei) of western Taymyr typical tundra subzone) (in Russian, with English summary). In: B.A. Tikhomirov (Editor), *Biogeotsenozy taimyrskoi tundry i ikh produktivnost, 2*. Nauka, Leningrad, pp. 148–151.

Ananjeva, S.I., Krivoluzkyi, D.A. and Chernov, Yu.I., 1979.

Pantsirnye kleshchi (Oribatei) v podzone arkticheskikh tundr na severo-vostoke Taimyra (Beetle mites (Oribatei) in arctic tundra subzone on north-east Taymyr). In: V.D. Aleksandrova and N.V. Matveyeva (Editors), *Arkticheskie tundry i poyarnye pustyni Taimyra*. Nauka, Leningrad, pp. 144–147.

Ananjeva, S.I., Babenko, A.B. and Chernov, Yu.I., 1987. Nogokhostiki (Collembola) v arkticheskikh tundrakh Taimyra (Sprintails (Collembola) in Taymyr arctic tundras) (in Russian, with English summary). *Zool. Zh.*, 66(7): 1038–1044.

Andreyev, M.P., 1983. Lishainiki ostrova Chetyrekhstolbovogo (Medvezhyi ostrova, Vostochno-Sibirskoe more) (Lichens of Chetyrekhstolbovoi island (Medvezhyi islands, Vostochno-Siberskoe sea) (in Russian, with English summary). *Nov. Sist. Nizshikh rast.*, 20: 133–139.

Andreyev, M.P., 1984a. Lishainiki poluostrova Yamal (Lichens of Yamal peninsula) (in Russian, with English summary). *Nov. Sist. Nizshikh Rast.*, 21: 127–136.

Andreyev, M.P., 1984b. Sistematicheskyi sostav likhenoflory Anyuiskogo nagorya (Systematical composition of Anyui plateau lichen flora) (in Russian, with English summary). *Nov. Sist. Nizshikh Rast.*, 21. 135–140.

Andreyev, V.N., 1932. Podzony tundr Severnogo Kraya (Tundra subzones of northern territories). *Priroda*, 10: 890–906.

Andreyev, V.N., 1935. Rastitelnost i prirodnye raiony vostochnoi chasti Bolshezemelskoi tundry (Vegetation and nature regions of the eastern part of Bolshezemelskaya tundra). *Tr. Polyarn. Kom. AN SSSR*, 22: 1–97.

Andreyev, V.N., 1938. Obsledovanie tundrovykh olenikh pastbishch s pomoshchyu samoleta (Observation of tundra reindeer pastures by means of airplane). *Tr. Polyarn. Zemled. Zhivotnovod i Promysl. Khoz. Olenevodstva*, 1: 1–172.

Andreyev, V.N., 1955. Deshifrirovanie po aerofotosnimkam razlichnykh tipov tundr i ikh aerovizualnaya kharakteristika po moroznoi treshchinovatosti (Identification of tundra vegetation types by means of airphotographs and their airvisual characteristics on frozen crack net). In: *Geograficheskyi shornik*, 7. Moskva-Leningrad. pp. 103–120.

Andreyeva, T.R., 1989. Pishchevye svyazi kulikov plakornykh tundr Yuzhnogo Yamala (Trophic relations of snipes in "plakor" tundras of Yuzhnyi Yamal). In: Yu.I. Chernov (Editor), *Ptitsy v soobshchestvakh tundrovoi zony*. Nauka, Moskva, pp. 129–152.

Archegova, I.B., 1985. *Gumusoobrazovanie na severe Evropeiskoi tundry SSSR (Humus Formation in the North European Tundras)*. Nauka, Leningrad, 136 pp.

Atlas Arktiki (Arctic Atlas), 1985. Moskva, 204 pp.

Atlas Okeanov. Severnyi Ledovityi okean (Ocean Atlas. Arctic Ocean), Moskva, 184 pp.

Avramchik, M.N., 1937. Geobotanicheskaya i pastbishchnaya kharakteristika raiona reki Dudypty (Geobotany and pasture characteristics of the Dudypta river region). *Tr. Arkt. Inst.*, 63: 47–81.

Bab'eva, I.P. and Chernov, I.Yu., 1982. Drozhzhi v tundrovykh pochvakh Taimyra (Yeasts in Taymyr tundra soils). *Pochvovedenie*, 10: 60–64.

Baer, K.M., 1838. Ekspeditsiya na Novuyu Zemlyu i Laplandiyu (Expedition to Novaya Zemlya and Lapland) (in Russian, with English summary). *Zh. Minist. Nar. Prosveshchenya*, 18(5): 1–87.

Batzli, G.O., 1975. The role of small mammals in arctic ecosystems. In: *Small Mammals: Their Productivity and Population Dynamics*. Vol. 5. Cambridge University Press, pp. 243–268.

Bazilevich, N.I., Grebenshchikov, O.S. and Tishkov, A.A. (1986). *Geograficheskie zakonomernosti struktury i funtsionirovaniya ekosistem (Geographical Pattern of Ecosystem Structure and Function)*. Nauka, Moskva, 296 pp.

Belopolskyi, L.O. (1957. *Ekologiya morskikh kolonialnykh ptits Barentsova morya (Ecology of Marine Colony Birds in the Barents Sea)*. Yu.I. Isakov (Editor), Nauka, Moskva-Leningrad, 458 pp.

Berg, B., 1984. Decomposition of moss litter in a mature Scotch pine forest. *Pedobiologia*, 26(5): 301–308.

Berg, L.S., 1928. Zona tundry (The tundra zone). *Izv. Leningr. Univ.*, 1: 191–233.

Berman, D.I., 1986. Fauna i naselenie bespozvonochnykh zhivotnykh tundro-stepnykh gruppirovok ostrova Vrangelya (Invertebrate fauna and population of Vrangel Island tundra-steppe). In: F.B. Chernyavskyi and I.A. Chereshnev (Editors), *Biogeografiya Beringyiskogo sektora Subarktiki*. Vladivostok, pp. 146–160.

Birulya, A.A., 1907. Ocherki iz zhizni ptits polyarnogo poberezhya Sibiri (Essay of bird life on polar coastal Siberia). *Zap. Imp. Akad. Nauk.*, 8,18(2): 1–157.

Blagodatskikh, L.S., 1973. Listostebelnye mkhi raiona Taimyrskogo stationara (zapadnyi Taimyr). (Mosses in the vicinity of Taymyr station (western Taymyr) (in Russian, with English summary). In: B.A. Tikhomirov (Editor), *Biogeotsenozy taimyrskoi tundry i ikh produktivnost, 2*. Nauka, Leningrad, pp. 107–119.

Blagodatskikh, L.S., Zhukova, A.L. and Matveyeva, N.V., 1979a. K flore listostebelnykh i pechenochnykh mkhov okrestnostei bukhty Marii Pronchishcheva (severo-vostochnyi Taimyr) (Flora of mosses and liverworts in the vicinity of the Maria Pronchishcheva (north-easthern Taymyr)). In: V.D. Aleksandrova and N.V. Matveyeva (Editors). *Arkticheskie tundry i polyarnye pustyni Taimyra*. Nauka, Leningrad, pp. 133–139.

Blagodatskikh, L.S., Zhukova, A.L. and Matveyeva, N.V., 1979b. Listostebelnye i pechenochnye mkhi mysa Chelyuskin (Mosses and liverworts of cape Chelyuskin). In: V.D. Aleksandrova and N.V. Matveyeva (Editors), *Arkticheskie tundry i polyarnye pustyni Taimyra*. Nauka, Leningrad, pp. 54–60.

Boch, M.S., 1974. Bolota tundrovoi zony Sibiri (printsipy tipologii) (Bogs of the Siberian tundra zone (principles of typology)). In: T.G. Abramova (Editor), *Tipy bolot SSSR i printsipy ikh klassifikatsii*. Nauka, Leningrad, pp. 146–154.

Boch, M.S., 1980. Bolota Taimyrskogo stationara (pos. Tareya) i ego okrestnostei (Bogs of the vicinity of the Taymyr station Tareya). In: B.A. Tomilin (Editor). *Biogeotsenozy taimyrskoi tundry*. Nauka, Leningrad, pp. 47–58.

Botch, M.S. and Masing, V.V., 1983. Mire ecosystems in the USSR. In: D. Goodall (Series Editor), *Ecosystems of the World*, Vol. 4. A. Gore (Volume Editor), *Mires: Swamp, Bog, Fen and Moor*. Elsevier, Amsterdam, pp. 95–152.

Bogacheva, I.A., 1982. Energetika razvitiya nekotorykh listogryzushchick nasekomykh Severa pri raznykh temperaturakh (Energy of development of some northern leaf-eating insects under different temperatures). *Ekologiya*, 5: 55–61.

Borkin, L.Ya., Belimov, G.T. and Sedalishchev, V.T., 1984. Novye dannye o rasprostranenii amfibyi i reptilyi v Yakutii (New data on the distribution of amphibians and reptiles in

Yakutia). In: L.Ya. Borkin (Editor), *Ekologiya i faunistika amfibyi, reptilyi SSSR i sopredelnykh stran*. Nauka, Leningrad, pp. 89–101.

Brotherus, V.E., 1910. Die Moose des Arktischen Küstengebietes von Sibirien. *Zap. Imp. Akad. Nauk.*, 8, 27(2): 1–15.

Budyko, M.I., 1956. *Teplovoi balans zemnoi poverkhnosti (Heat Balance of the Globe Surface)*. Leningrad. 255 pp.

Bulavintsev, V.I. and Babenko, A.B., 1983. Pochvennye bespozvonochnye v vostochnom sektore arkhipelaga Zemlya Frantsa-Iosifa (Soil invertebrates in eastern sector of Franz-Josef archipelago) (in Russian, with English summary). *Zool Zh.*, 62(7): 1114–1116.

Ceika, B., 1910, 1912, 1914. Die Oligochaeten der russischen in der Jahren 1900–1903 unternommen Nordpolarexpedition. *Zap. Imp. Akad. Nauk.*, 8,29(2): 1–38; (6): 19–45; (9): 1–23

Chastukhina, S.A., 1984. Tsenoticheskaya rol *Novosieversia glacialis* (Rosaceae) v gornykh driadovykh tundrakh plato Putorana (Coenotical role of *Novosieversia glacialis* (Rosaceae) in mountain *Dryas* tundra in the Putorana plateau) (in Russian, with English summary) *Bot. Zh.*, 69(3): 399–403.

Chernov, I Yu., 1985. Sinekologicheskyi analiz gruppirobok drozhzhei taimyrskoi tundry (Synecological analysis of yeasts in Taymyr tundra). *Ekologiya*, 1. 54–60.

Chernov, I.Yu. and Bab'eva, I P., 1988. Novyi vid drozhzhey r. Cryptococcus iz tundrovykh pochv (New yeast species of the genus *Gryptococcus* i tundra soils). *Microbiologiya*, 57(6): 1031–1034.

Chernov, Yu.I., 1961. K izucheniyu zhivotnogo naseleniya pochv arkticheskikh tundr Yakutii (Study of soil animal populations in Yakutian arctic tundras) (in Russian, with English summary). *Zool. Zh.*, 40(3): 326–333.

Chernov, Yu.I., 1964. Zavisimost sostava zhivotnogo naseleniya pochv i derniny ot kharaktera rastitelnogo pokrova v nekotorykh tipakh tundr (Dependence of soil and turf animal population composition on vegetation cover in some tundras). *Prob Severa*, 8: 254–267.

Chernov, Yu.I., 1965. Kompleks sinantropnykh dvukrylykh v tundrovoi zone (Synanthropous dipterans in the tundra zone). *Entomol. Obozr.*, 44(1): 74–83.

Chernov, Yu.I., 1966. Kompleks antofilnykh nasekomykh v tundrovoi zone (Anthophilous insects in the tundra zone). In: A.G. Voronov (Editor), *Organizmy i prirodnaya sreda (Voprosy geografii, 69)*. Moskva, pp. 76–97.

Chernov, Yu.I., 1967. Troficheskie svyazi ptits s nasekomymi v tundrovoi zone (Trophic interrelations between birds and insects in the tundra zone). *Ornitologiya*, 8: 133–149.

Chernov, Yu.I., 1973a. Geozoologicheskaya kharakteristika territorii Taimyrskogo biogeotsenologicheskogo stationara (Geozoological characteristics of the Taymyr biogeocoenological station areas) (in Russian, with English summary). In: B.A. Tikhomirov (Editor), *Biogeotsenozy taimyrskoi tundry i ikh produktivnost, 2*. Nauka, Leningrad, pp. 187–200.

Chernov, Yu.I., 1973b. Kratkyi obzor troficheskikh grupp bespozvonochnykh tipichnykh tundr zapadnogo Taimyra (A brief outline of trophic groups of invertebrates in the typical tundra subzone of western Taymyr). In: B.A. Tikhomirov (Editor), *Biogeotsenozy Taymyrskoi tundry i ikh produktivnost*. Nauka, Leningrad, pp. 166–179.

Chernov, Yu.I., 1975. *Prirodnaya zonalnost i zhivotnyi mir sushi (Natural Zonation and the Terrestrial Animal World)*. Mysl, Moskva, 222 pp.

Chernov, Yu.I., 1978a. Antofilnye nasekomye v podzone tipichnykh tundr Zapadnogo Taimyra i ikh rol v opylenii rastenyi (Anthophilous insects in the typical tundra subzone of western Taymyr and their role in plant pollination). In: B.A. Tikhomirov and B.A. Tomilin (Editors), *Struktura i funktsii biogeotsenozov taimyrskoi tundry*. Nauka, Leningrad, pp. 264–290

Chernov, Yu.I., 1978b. *Struktura zhivotnogo naseleniya Subarktiki (Structure of the Animal Population in the Subarctic)* (in Russian, with English summary). Nauka, Moskva, 167 pp.

Chernov, Yu.I., 1980. *Zhizn tundry (The Living Tundra)*. Mysl, Moskva, 236 pp. (English translation: *The Living Tundra*. 1985. Cambridge University Press. 213 pp.).

Chernov, Yu.I., 1982. O putyakh i istochnikakh formirovaniya fauny malykh ostrovov Okeanii (On the pathways and sources of fauna formation on small islands of Oceania) (in Russian, with English summary). *Zh Obshch. Biol.*, 13(1): 35–47.

Chernov, Yu.I., 1984a. Biologicheskie predposylki osvoeniya arkticheskoi sredy organizmami razlichnykh taksonov (Biological preconditions of settling the arctic environments by different taxa). In: Yu.I. Chernov (Editor), *Faunogenez i filotsenogenez*. Nauka, Moskva, pp. 154–174

Chernov, Yu.I., 1984b. Evolutsionnyi protsess i istoricheskoe razvitie soobshchestv (Evolutionary process and historical development of communities). In: Yu.I. Chernov (Editor), *Faunogenez i filotsenogenez*. Nauka, Moskva, pp. 5–23.

Chernov, Yu.I., 1985. Sreda i soobshchestva tundrovoi zony (Environments and communities in the tundra zone) (in Russian, with English summary). In: Yu.I. Chernov (Editor), *Soobshchestva Krainego Severa i chelovek*. Nauka, Moskva, pp. 8–22.

Chernov, Yu.I., 1988. Filogeneticheskyi uroven i geograficheskoe raspredelenie taksonov (Phylogenetic level and geographical distribution of taxa) (in Russian, with English summary) *Zool. Zh.*, 67(10): 1445–1458.

Chernov, Yu.I., 1989. Teplovye usloviya i biota Arktiki (Heat conditions and Arctic biota). *Ekologiya*, 2: 49–57.

Chernov, Yu.I., 1992. Kogo bolshe v tundre - khishchnikov ili fitofagov? (Who are more numerous in tundra - predators or phytophages?) In: Yu.I. Chernov (Editor), *Tsenoticheskie vzaimodeistviya v tundrovykh ekosistemakh*. Nauka, Moskva, pp. 100–125.

Chernov, Yu.I. and Khlebosolov, E.I., 1989. Troficheskie svyazi i vidovaya struktura naseleniya tundrovykh kulikov (Trophic relations and species structure of tundra snipe populations). In: Yu.I. Chernov (Editor), *Ptitsy v soobshchestvakh tundrovoi zony*. Nauka, Moskva, pp. 39–51.

Chernov, Yu.I. and Matveyeva, N.V., 1979. Zakonomernosti zonalnogo raspredeleniya soobshchestv na Taimyre (The regularities of community zonal distribution on Taymyr). In: V.D. Aleksandrova and N.V. Matveyeva (Editors). *Arkticheskie tundry i polyarnye pustyni Taimyra*. Nauka, Leningrad, pp. 166–200.

Chernov, Yu.I. and Matveyeva, N.V., 1986. Yuzhnye tundry v sisteme zonalnogo deleniya (Southern tundras in the zonal division system). In: Yu.I. Chernov and N.V. Matveyeva (Editors). *Yuzhnye tundry Taimyra*. Nauka, Leningrad, pp. 192–204.

Chernov, Yu.I., Ananjeva, S.I. and Khajurova, E.P., 1971. Kompleks pochvoobitayushchich bespozvonochnykh c pyatnistykh tundrakh Zapadnogo Taimyra (Soil invertebrates in

western Taymyr frost-boil tundras) (in Russian, with English summary). In: B.A. Tikhomirov (Editor), *Biogeotsenozy taimyrskoi tundry i ikhy produktivnost*. Nauka, Leningrad, pp. 198–211.

Chernov, Yu.I., Ananjeva, S.I., Kuzmin, L.L. and Khayurova, E.P., 1973. Nekotorye osobenosti vertikalnogo raspredeleniya bespozvonochnykh v pochvakh tundrovoi zony (Some peculiarities of invertebrate vertical distribution in soils of the tundra zone) (in Russian, with English summary). In: B.A. Tikhomirov (Editor), *Biogeotsenozy taimyrskoi tundry i ikh produktivnost, 2*. Nauka, Leningrad, pp. 180–186.

Chernov, Yu.I., Striganova, B.R. and Ananjeva, S.I., 1977. Soil fauna of the polar desert at cape Chelyuskin, Taymyr peninsula, USSR. *Oikos*, 29: 175–179.

Chernov, Yu.I., Striganova, B.R., Ananjeva, S.I. and Kuzmin, L.L., 1979. Zhivotnyi mir polyarnoi pustyni mysa Chelyuskin (Animal world of polar desert at cape Chelyuskin). In: V.D. Aleksandrova and N.V. Matveyeva (Editors), *Arkticheskie tundry i polyarnye pustyni Taimyra*. Nauka, Leningrad, pp. 35–49.

Chernov, Yu.I., Matveyeva, N.V and Zanokha, L.L., 1983. Opyt izucheniya prirosta tsvetkovykh rastenyi v soobshchestvakh Taimyra (The experience of studying vascular plant productivity in Taymyr plant communities). *Dokl. AN SSSR*, 272(4): 999–1002.

Chernyavskyi, F.B., 1985. *Mlekopitayushchie Krainego Severa Sibiri (Mammals of the Siberian Far North)*. Nauka, Moskva, 388 pp.

Chernyavskyi, F.B. and Dorogoi, I.V., 1988. Vzaimootnosheniya khishchnikov-miofagov i lemmingov v arkticheskikh ekosistemakh (na primere o. Vrangelya) (Relationships between predators-miophages and lemmings in arctic ecosystems (with Vrangel island as an example). *Zh. Obsh. Biol.*, 59(6): 813–824.

Chernyavskyi, F.B. and Tkachev, A.V., 1982. *Populyatsionnye tsikly lemmingov v Arktike (Lemming Population Cycles in the Arctic)*. Nauka, Moskva, 162 pp.

Danilov, N.N., 1966. *Puti prisposobleniya nazemnykh zhivotnykh k usloviyam sushchestvovaniya v Subarktike. II. Ptitsy (Ways of Adaptations of Terrestrial Animals to Environments in Subarctic. II. Birds)*. Sverdlovsk, 147 pp.

Danilov, N.N., Ryzhanovskyi, V.N. and Ryabtsev, V.K., 1984. *Ptitsy Yamala (Birds of Yamal)*. Nauka, Moskva, 332 pp.

Danks, H.V., 1981. *Arctic Arthropods*. Entomological Society of Canada, Ottawa, 608 pp.

Deyeva, N.M., 1980. Sezonnoe razvitie rastenyi i rastitelnykh soobshchestv Taimyrskogo biogeotsenologicheskogo stationara (Seasonal development of plants and communities in the vicinity of the Taymyr biogeoecoenological station). In: B.A. Tomilin (Editor), *Biogeotsenozy taimyrskoi tundry*. Nauka, Leningrad, pp. 59–96.

Dorogostaiskaya, E.V., 1959. K voprosu o pochvennoi algoflore pyatnistykh tundr Krainego Severa (On the problem of algae flora of frost-boil tundras of the Far North) (in Russian, with English summary). *Bot. Zh.*, 44(3): 312–321.

Dorogostaiskaya, E.V., 1972. *Sornye rasteniya Krainego Severa (Weeds of the USSR Far North)*. Nauka, Leningrad, 187 pp.

Dorogostaiskaya, E.V. and Sdobnikova, N.V., 1973. Pochvennye vodorosli tundr zapadnogo Taimyra (Soil algae of western Taymyr tundras) (in Russian, with English summary). In: B.A. Tikhomirov (Editor), *Biogeotsenozy taimyrskoi tundry i ikh produktivnost, 2*. Nauka, Leningrad, pp. 128–138.

Druzhinina, O.A., 1985. Dinamika rastitelnosti v raionakh intensivnogo osvoeniya Krainego Severa (Vegetation dynamics in the northern region under intensive impact by man) (in Russian, with English summary). In: Yu.I. Chernov (Editor), *Soobshchestva Krainego Severa i chelovek*. Nauka, Moskva, pp. 205–231.

Druzhinina, O.A. and Zharkova, Yu.I., 1979. A study of plant communities of anthropogenic habitats in the area of Vorkuta industrial center. *Biol. Pap. Univ. Alaska*, 20: 30–53.

Dunaeva, T.N., 1948. Sravnitelnyi obzor ekologii tundrovykh polevok (A comparative review of the ecology of tundra voles). *Tr. Inst. Geogr.*, 41: 78–155.

Dunaeva, T.N., 1978. K ekologii lemmingov v severo-zapadnoi Yakutii (On the lemming ecology in the north-western Yakutia). *Byull. Mosk. O. Ispyt. Prir.*, 83(2): 18–26.

Dunaeva, T.N., 1985. Prirodoochagovye bolezni na Krainem Severe (Natural focal diseases in the Extreme North). In: Yu.I. Chernov (Editor), *Soobshchestva Krainego Severa i chelovek*. Nauka, Moskva, pp. 134–169.

Elenkin, A.A., 1909. Lishainiki polyarnogo poberezhya Sibiri (Lichens of the Siberian polar coast). *Zap. Imp. Akad. Nauk.*, 8,27(1): 1–53.

Eskov, K.Yu., 1985. Pauki tundrovoi zony SSSR (Spiders in the USSR tundra zone). In: V.I.Ovcharenko (Editor), *Fauna i ekologiya paukov SSSR. (Tr. Zool. Inst., 39)*. Leningrad, pp. 121–128.

Eskov, K.Yu., 1986. Fauna paukov (Aranei) gipoarcticheskogo poyasa Sibiri (Spider (Aranei) fauna of the hypoarctic belt of Siberia). In: Yu.I. Chernov and N.V. Matveyeva (Editors), *Yuzhnye tundry Taimyra*. Nauka, Leningrad, pp. 175–191.

Flanagan, P. and Bunell, F., 1980. Microflora activities and decomposition. In: J. Brown, P.C. Miller, L.L. Tieszen, F.L. Bunell (Editors), *An Arctic Ecosystem (The Coastal Tundra at Barrow, Alaska)*. Dowden, Hatchinson and Ross, Inc., Stroudsburg, PA, pp. 291–234.

Fridland, V.M., 1972. *Struktura pochvenogo pokrova (The structure of soil cover)*. Nauka, Moskva, 223 pp.

Fridolin, V.Yu., 1936. Zhivotno-rastitelnoe soobshchestvo gornoi strany Khibin (Animal-plant communitiey of Khibiny mountains). *Tr. Kolskoi bazy AN SSSR*, 3: 1–296.

Gavrilova, M.K., 1981. *Sovremennyi klimat i vechnaya merzlota na kontinentakh (Recent Climate and Permafrost on Continents)*. Nauka SO, Novosibirsk, 112 pp.

Gavrilyuk, V.A., 1961. Prodolzhitelnost perioda plodonosheniya i semennaya produktivnost na yugo-vostoke Chukotki (Duration of the fruiting period and seed production in the southeastern Chukotka) (in Russian, with English summary). *Bot. Zh.*, 46(1): 90–97.

Gerasimenko, T.V. and Shvetsova, V.M., 1988. Osnovnye resultaty izuqueniya fotosinteza v Arktiki (Main results of ecophysiological investigations of photosynthesis in the Arctic). In: O.A. Semikhatova (Editor), *Ekofiziologicheskie issledovaniya fotosinteza i dykhaniya rastenyi*. Nauka, Leningrad, pp. 65–114.

Gerasimenko, T.V. and Zalenskyi, O.V., 1973. Sutochnaya i sezonnaya dinamika fotosinteza rastenyi o. Vrangelya (Diurnal and seasonal dynamics of photosynthesis of Vrangel island plants) (in Russian, with English summary). *Bot. Zh.*, 58(11): 1655–1666.

Gerasimenko, T.V., Deyeva, N.M., Gagen, T.K. and Zalenskyi, O.V., 1980. Potenstialnyi fotosyntez rastenyi Zapadnogo

Taimyra (Potential photosynthesis of western Taymyr plants). In: B.A. Tomilin (Editor), *Biogeotsenozy taimyrskoi tundry*. Nauka, Leningrad, pp. 145–164

Gerasimenko, T.V., Popova, I.A., Aleksandrova, N.M. and Gagen, T.K., 1988. Soderjanie khlorofilla i fotosintez u rastenyi ostrova Vrangelya vtequenie ikhvegetatsii (Chlorophyll content and photosynthesis in plants of the Vrangel island in the course of their growing). *Bot. Zh.*, 73: 1085–1103.

Gerasimenko, T.V., Popova, I.A. and Aleksandrova, N.M., 1989. Kharakteristika fotosinteticheskogo apparata i fotosinteza rastenyi arktiqueskoi tundry (ostrov Vrangelya) (On characterization of the photosynthetic apparatus and photosynthesis in plants of the arctic tundra (Vrangel island)). *Bot Zh.*, 74: 669–679.

Getsen, M.V., 1985. *Vodorosli v ekosistemakh Krainego Severa (Algae in Ecosystems of the Extreme North)*. Nauka, Moskva, 165 pp.

Getsen, M.V. and Kostyaev, V.Ya., 1989. *Ekologiya azotfiksatsii v tundre (Ecology of nitrogen fixation in tundra)*. Syktyvkar. 24 pp.

Giljarov, A.M., 1969. Sootnoshenie biomassy i vidovogo raznoobraziya v planktonnom soobshchestve (Biomass and species diversity in a plankton community) (in Russian, with English summary). *Zool. Zh.*, 48(4): 485–493.

Gorodkov, B.N., 1928. Krupnobugristye torfyaniki i ikh geograficheskoe rasprostranenie (Palsa peat bogs and their geographical distribution). *Priroda*, 6: 599–601.

Gorodkov, B.N., 1932. Vechnaya merzlota v severnom krae (Permafrost in the northern area). *Tr. Sov. Izuch. Proizvod AN SSSR, Seriya Sev.*, 1: 5–109.

Gorodkov, B.N., 1935. *Rastitelnost tundrovoi zony SSSR (Vegetation of the USSR Tundra Zone)*. Izd. AN SSSR, Moskva-Leningrad. 142 pp.

Gorodkov, B.N., 1938. Rastitelnost Arktiki i gornykh tundr SSSR (Vegetation of Arctic and mountain tundras of the USSR). In: Yu.D. Tsinzerling (Editor), *Rastitelnost SSSR, 1*. Izd. AN SSSR, Moskva-Leningrad. pp. 296–354.

Gorodkov, B.N., 1952. Analiz rastitelnosti zony arkticheskikh pustyn na primere ostrova Vrangelya (Analysis of vegetation of the arctic desert zone with the Vrangel island as an example). In: R.F. Gekker (Editor), *Krainyi Severo-Vostok Soyuza SSR, 1. Ostrov Vrangelya*. pp. 149–184.

Gorodkov, B.N., 1956. Rastitelnost i pochvy o Kotelnogo (Novosibirskyi arkhipelag) (Vegetation and soils of Kotelny island (Novosibirsky Archipelago)). In: B.A. Tikhomirov (Editor), *Rastitelnost Krainego Severa i ee osvoenie, 2*. Izd. AN SSSR, Moskva, pp. 7–132.

Gorodkov, B.N., 1958. Pochvenno-rastitelnyi pokrov ostrova Vrangelya (Soil-vegetation cover of Vrangel island). In: B.A. Tikhomirov (Editor), *Rastitelnost Krainego Severa i ee osvoenie, 3*. Izd. AN SSSR, Moskva-Leningrad, pp. 5–58.

Grigor'ev, A.A., 1956. *Subarktika (The Subarctic)*. Geografgiz, Moskva. 223 pp.

Grigor'ev, A.A., 1970. *Tipy geograficheskoi sredy (Types of Geographical Environments)*. Moskva, 468 pp.

Grunina, L.K. and Getsen, M.V., 1984a. *Biogennaya akkumulatsiya azota rasteniyami tundrovoi zony (Biogenic Nitrogen Accumulation by Tundra Plants)*. Syktyvkar. 31 pp.

Grunina, L.K. and Getzen, M.V., 1984b. Ekologo-tsenoticheskie svyazi v protsesse nakopleniya azota rasteniyami Krainego Severa (Ecologocenotical relations in the process of the nitrogen accumulation by northern plants). *Ekologiya*, 2: 33–37.

Hammer, M., 1952. Investigations on the microfauna of northern Canada. I. Oribatei. *Acta Arct.*, 4: 1–108.

Hammer, M., 1953. Investigations on the microfauna of northern Canada. II. Collembola. *Acta Arct.*, 6: 1–108.

Holmes, R.T., 1966. Feeding ecology of the red-backed sandpiper (*Calidris alpina*) in Arctic Alaska. *Ecology*, 47: 32–47.

Ignatenko, I.V., 1971. Pochvy osnovnykh tipov tundrovykh biogeotsenozov zapadnogo Taimyra (na primere stationara Botanicheskogo instituta) (Soils of the main tundra biogeocenoses at western Taymyr (with the station of Botanical Institute as an example)) (in Russian, with English summary). In: B.A. Tikhomirov (Editor), *Biogeotsenozy taimyrskoi tundry i ikh produktivnost*. Nauka, Leningrad, pp. 57–107.

Ignatenko, I.V., 1973. Poyasnitelnyi tekst k pochvennoi karte tundrovogo statsionara Botanicheskogo instituta AN SSSR (Legend to soil map of Botanical Institute AN USSR tundra station) (in Russian, with English summary). In: B.A. Tikhomirov (Editor), *Biogeotsenozy taimyrskoi tundry i ikh produktivnost, 2*. Nauka, Leningrad, pp. 50–57.

Isachenko, B.L., 1914. Issledovaniya nad sporonosnymi bakteriyami Severnogo Ledovitogo okeana (Study of spore bacteria of the Arctic Ocean). In: *Trudy Murmanskoi nauchnoi polyarnoi ekspeditsii 1906*. St. Petersburg, pp. 276–295.

Isachenko, B.L. and Simakova, T.L., 1934. Bakteriologicheskie issledovaniya pochv Arktiki (Bacteriological study of arctic soils). *Tr. Arkt. Inst.*, 9: 80–99.

Kalesnik, S.V., 1970. *Obshchie geograficheskie zakonomernosti Zemli (General Geographical Regularities at the Globe)*. Izd. AN SSSR, Moskva, 283 pp.

Kalyakin, V.I., 1989. Khishchnye ptitsy v ekosistemakh Krainego Severa (Birds in the ecosystems of the Far North). In: Yu.I. Chernov (Editor), *Ptitsy v soobshchestvakh tundrovoi zony*. Nauka, Moskva, pp. 51–112.

Kannukene, L.R. and Matveyeva, N.V., 1986. Listostebelnye mkhi okrestnostei pos. Kresty (podzona yuzhnykh tundr, zapadnyi Taimyr) (Mosses in the vicinity of Kresty (southern tundra subzone, western Taymyr)). In: Yu.I. Chernov and N.V. Matveyeva (Editors), *Yuzhnye tundry Taimyra*. Nauka, Leningrad, pp. 89–100.

Katenin, A.E., 1972. Mikoriza rastenyi Severo-Vostoka Evropeiskoi chasti SSSR (Mycorrhiza of plants in the north-east of the European part of the USSR). In: B.A. Tikhomirov (Editor), *Rastitelnost Krainego Severa i ee osvoenie, 12*. Nauka, Leningrad, pp. 1–140

Kertselli, S.V., 1911. *Po Bolshezemelskoi tundre s kochevnikami (Through the Bolshezemelskaya Tundra together with Nomads)*. Arkhangelsk, 116 pp.

Khantimer, I.S., 1974. *Selskokhozyaistvennoe osvoenie tundry (Agricultural Reclamation of Tundra)*. Nauka, Leningrad, 226 pp.

Khlebosolov, E.I., 1983. O troficheskoi izbiratelnosti u nekotorykh tundrovykh kulikov. (On the trophic selective ability of some tundra snipes) (in Russian, with English summary). *Zool. Zh.*, 62(6): 963–965.

Khlebosolov, E.I., 1986. Pishchevye resursy tundrovykh kulikov i osobennosti ikh povedeniya v reproduktivnyi periods (Food resources of snipes and their behavior during the reproductive period) (in Russian, with English summary). *Zool. Zh.*, 65(7): 1032–1040.

Khodachek, E.A., 1969. Rastitelnaya massa tundrovykh fitot-

senozov zapadnogo Taimyra (Phytomass in tundra cenoses at western Taymyr) (in Russian, with English summary). *Bot. Zh.*, 54(7): 1059–1073.

Khodachek, E.A., 1970. Semennaya produktivnost i urozhai semyan rastenyi v tundrakh zapadnogo Taimyra (Seed production and yield in western Taymyr tundras) (in Russian, with English summary). *Bot. Zh.*, 55(7): 995–1007.

Khodachek, E.A., 1978. Semennaya produktivnost rastenyi zapadnogo Taimyra (Seed production of western Taymyr plants). In: B.A. Tikhomirov and B.A. Tomilin (Editors), *Struktura i funktsii biogeotsenozov taimyrskoi tundry*. Nauka, Leningrad, pp. 166–197.

Khruleva, O.A., 1987. Bespozvonochnye zhivotnye (Invertebrate animals). In: V.E. Sokolov (Editor), *Flora i fauna zapovednikov SSSR. Fauna zapovednika Ostrov Vrangelya*. Nauka, Moskva, pp. 6–35.

Kildyushevskyi, I.D., 1956. Podsnezhnoe razvitie nekotorykh vidov flory Malogo Yamala (Development under snow of some species in Malyi Yamal) (in Russian, with English summary). *Bot. Zh.*, 41(11): 1641–1646.

Kirichenko, A.I., 1960. Nastoyashchie polyzhestkokrylye (Heteroptera) vostochnogo sektora Arkticheskoi Evrasii (True bugs (Heteroptera) of eastern part of Arctic Eurasia). *Entomol. Obozr.*, 39(3): 617–628.

Kiryushchenkmo, S.P., 1979. Vozdeistvie lemmingov na rastitelnost arkticheskoi ekosistemy (na primere o. Vrangelya) (The influence of lemmings on vegetation of arctic ecosystems (with Vrangel island as an example)). In: V.G. Krivosheyev (Editor), *Ekologiya polevok i zemleroek na Severo-Vostoke Sibiri*. Nauka OVO, Vladivostok, pp. 39–49.

Kiryushchenko, S.P. and Kiryushchenko, T.V., 1979. Pitanie sibirskikh (*Lemmus sibiricus*) i kopytnykh (*Dicrostonyx torquatus*) lemmingov na o. Vrangelya (The food of lemmings *Lemmus sibiricus* and *Dicrostonyx torquatus* on Vrangel island). In: V.G. Krivosheev (Editor), *Ekologiya polevok i zemleroek na Severo-Vostoke Sibiri*. Nauka OVO, Vladivostok, pp. 25–38.

Kiselev, S.V., 1981. *Pozdnekainozoiskie zhestkokrylye severo-vostoka Sibiri. (Late Kainosoie Coleopterans of Northeast Siberia)*. Nauka, Moskva, 115 pp.

Kishchinskyi, A.A., 1971. Sovremennoe sostoyanie populyatsii dikogo severnogo olenya na Novosibirskykh ostrovakh (Recent state of northern reindeer population on Novosibirskie islands) (in Russian, with English summary). *Zool. Zh.*, 50(1): 117–122.

Kishchinskyi, A.A., 1974. Arktoalpyiskaya avifauna i ee proiskhozhdenie (Arctic avifauna and its origin) (in Russian, with English summary). *Zool. Zh.*, 53(7): 1036–1051.

Kishchinskyi, A.A., 1976. Chislennost, biomassa ptits i transformatsiya imi energii v subarkticheskikh ekosistemakh (Numbers, biomass of birds and their energy transformation) (in Russian, with English summary). *Ekologiya*, 5: 71–78.

Kishchinskyi, A.A., 1978. Troficheskie vzaimootnosheniya ptits i nekotorykh bespozvonochnykh v tundrovykh ekosistemakh (Trophic relationships between birds and some invertebrates in tundra ecosystems). *Zh. Obshch. Biol.*, 39(2): 212–226.

Kjelvik, S., Wielgolaski, F.E. and Jahren, A., 1975. Photosynthesis and respiration of plants studied by field technique at Hardangervidda, Norway. In: F.E. Wielgolaski (Editor), *Fennoscandian Tundra Ecosystems. Part I. Plants and Microorganisms*. Springer Verlag, Berlin-Heidelberg-New York, pp. 184–193.

Kolpashchikov, L.A., 1989. *Dikyi severnyi olen Taimyra (The Wild Reindeer on Taymyr)*. Norilsk, 23 pp.

Kontrimavichus, V.L. (Editor), 1975. *Paraziticheskie organizmy Severo-Vostoka Azii (Parasitic Organisms in Northeast Asia)*. Nauka OVO, Vladivostok, 178 pp.

Korobkov, A.A., 1985. Vidovoi sostav rastenyi na silno narushennykh uchastkakh v basseine Anadyrya (The floristic composition of the disturbed area in the Anadyr river basin) (in Russian, with English summary). In: Yu.I. Chernov (Editor), *Soobshchestva Krainego Severa i chelovek*. Nauka, Moskva, pp. 231–244.

Korotyaev, B.A., 1980. Materialy po faune zhukov-dolgonosikov (Coleoptera, Curculionidae) Severo-Vostoka SSSR (Data on the weevil (Coleoptera, Curculionidae) fauna in northeastern USSR). In: L.N. Medvedev (Editor), *Issledovaniya po entomofaune Severo-Vostoka SSSR*. Nauka OVO, Vladivostok, pp. 23–50.

Koshkina, T.V., 1970. O faktorakh dinamiki chislennosti lemmingov (On the factors of dynamic of lemmings numbers). In: A.P. Formozov (Editor), *Fauna i ekolgiya gryzunov*, 9. Izd. MGU, pp. 11–61.

Kovakina, V.A., 1952. O perezimovani nekotorykh zlakov na Krainem Severe (On the hibernation of some grasses at the Extreme North). *Bot. Zh.*, 37(5): 684–698.

Kovakina, V.A., 1958. Biologicheskie osobennosti nekotorykh zimnezelenykh rastenyi Krainego Severa (Biological peculiarities of some wintergreen plants at the Extreme North) (in Russian, with English summary). *Bot. Zh.*, 43(9): 1326–1332.

Kozhevnikov, Yu.P., 1986. Sosudistye rasteniya (Vascular plants). In: B.N. Norin (Editor), *Gornye fitotsenoticheskie sistemy Subarktiki*. Nauka, Leningrad, pp. 45–77.

Kozlovskaya, L.S., 1955. K kharakteristike pochvennoi fauny Bolshezemelskoi tundry (On soil fauna in Bolshezemelskaya tundra). *Dokl. AN SSSR*, 104(3). 485–485.

Kozlovskaya, L.S., 1976. *Rol bespozvonochnykh v transformatsii organicheskogo veshchestva bolotnykh pochv (The role of invertebrates in the transformation of the organic matter in bog soils)*. Nauka, Leningrad, 211 pp.

Krebs, C.J., 1964. The lemming cycle at Baker Lake, Northwest Territories, during 1959–1962. *Arct. Inst. North Am. Tech. Pap.*, 15: 1–104.

Krechmar, A.V., 1966. Ptitsy Zapadnogo Taimyra (Birds of western Taymyr). *Tr. Zool. Inst. AN SSSR*, 39: 185–311.

Krechmar, A.V., Andreyev, A.V. and Kondratjev, A.Ya., 1978. *Ekologiya i rasprostranenie ptits na severo-vostoke SSSR (Ecology and Distribution of Birds in Northeast USSR)*. Nauka, Moskva, 194 pp.

Kriss, A.E., 1947. Mikroorganizmy tundrovykh i polyarnopustynnykh pochv Arktiki (Microorganisms of arctic tundra and polar desert soils). *Mikrobiologiya*, 16(5):437–438.

Kriss, A.E., 1952. Kolichestvennaya i vidovaya kharakteristika mikroorganismov tundrovykh i arkto-pustynnykh pochv ostrovov Vrangelya, Kolyuchin i Chukotskogo polyostrova (Quantity and species characteristics of tundra and polar desert soil microorganisms of Vrangel and Kolyuchin islands and Chukotka peninsula). In: R.S. Gekker (Editor), *Krainyi Severo-Vostok Souyza SSR, 1*. Izd. AN SSSR. Ostrov Vrangelya. Moskva-Leningrad, pp. 185–207.

Kryuchkov, V.V., 1976. *Chutkaya Subarktika (The Sensitive Subarctic)*. Nauka, Moskva, 136 pp.

Kryuchkov, V.V., 1979. *Sever: priroda i chelovek (North: Nature and Man)*. Nauka, Moskva, 127 pp.

Kuzmin, L.L., 1973. Fauna svobodnozhivushchikh nematod Zapadnogo Taimyra (Fauna of free-living nematodes at western Taymyr) (in Russian, with English summary). In: B.A. Tikhomirov (Editor), *Biogeotsenozy taimyrskoi tundry i ikh produktivnost, 2*. Nauka, Leningrad, pp. 139–147.

Kuzmin, L.L., 1978. Ekologiya svobodnozhivushchikh nematod podzony tipichnykh tundr Zapadnogo Taimyra (Ecology of free-living nematods of the western Taymyr typical tundra subzone). In: B.A. Tikhomirov and B.A. Tomilin (Editors), *Struktura i funktsii biogeotsenozov taimyrskoi tundry*. Nauka, Leningrad, pp. 228–244.

Kuzmin, L.L., 1986. Svobodnozhivushchie nematody v podzone yuzhnykh tundr zapadnogo Taimyra (Free-living nematodes in the western Taymyr southern tundra subzone). In: Yu.I. Chernov and N.V. Matveyeva (Editors), *Yuzhnye tundry Taimyra*. Nauka, Leningrad, pp. 118–121.

Kuznetsov, N.Ya., 1938. Arkticheskaya fauna Evrasii i ee proiskhozhdenie (Arctic fauna and its origin). *Tr. Zool. Inst.*, 5(1): 1–185.

Kuznetsova, N.A., 1985. Gruppirovki kollembol v ekologicheskom ryadu elnikov yuga Arkhangelskoi oblasti (Springtail complexes in ecological range of fir forests in the south of Archangel district). In: M.S. Gilyarov and N.M. Chernova (Editors), *Fauna i ekologiya nogokhvostok*. Nauka, Moskva, pp. 68–77.

Lantsov, V.I. and Chernov, Yu.I., 1987. *Tipuloidnye dvukrylye v tundrovoi zone (Tipuloid Diptera in the Tundra Zone)*. Nauka, Moskva, 176 pp.

Lebedeva, L.A., 1928. Griby arkticheskogo poberezhya Sibiri (Fungi of the arctic coast of Siberia). *Tr. Kom Izuch. YaSSR*, 12: 8–16.

Lind, J., 1927. The geographical distribution of some arctic micromycetes. *K. Dan Vidensk Selsk. Biol. Medd.*, 6(5): 17–22.

Lind, J., 1934. Studies on the geographical distribution of arctic circumpolar micromycetes. *K. Dans. Vidensk Selsk. Biol Medd.*, 11(2): 152.

Litvin, K.E. and Baranyuk, V.V., 1989. Razmnozhenie belykh sov (*Nyctea scandiaca*) i chislennost lemmingov na ostrove Vrangelya (The reproduction of snowy owls (*Nyctea scandiaca*) and numbers of lemmings on Vrangel Island). In: Yu.I. Chernov (Editor), *Ptitsy v soobshchestvakh tundrovoi zony*. Nauka, Moskva, pp. 112–129.

Litvin, K.E. and Ovsyanikov, N.G., 1990. Zavisimost razmnozhenya i chislennosti belykh sov i pestsov ot chislennosti lemmingov na ostrove Vrangelya (The dependence of breeding and numbers of snowy owls and arctic foxes on the numbers of lemmings on Vrangel Island) (in Russian, with English summary). *Zool. Zh.*, 69(4): 52–64.

Litvin, K.E., Pulyaev, A.I. and Syroechkovsky, E.V., 1985. Naselenie belogo gusya, chernoi kazarki i obyknovennoi gagi vblizi gnezd polyarnoi sovy na ostrove Vrangelya (Populations of white goose, brent goose and common eider near the nests of polar owls at Vrangel island) (in Russian, with English summary). *Zool. Zh.*, 64(7): 1012–1023.

Liverovsky, Yu.A., 1934. Pochvy tundr severnogo kraya (Tundra soils of the northern area). *Tr. Polyarn. Kom. AN SSSR*, 19: 1–112.

Lovelius, N.V., 1978. Snezhny pokrov i merzlota (Snow cover and permafrost). In: B.N. Norin (Editor), *Ary-Mas. Prirodnye usloviya, flora i rastitelnost*. Nauka, Leningrad, pp. 21–30.

Lozina-Lozinskyi, L.K., 1972. *Ocherki po kriobiologii (Outlines on Cryobiology)*. Nauka, Leningrad, 137 pp.

Luxton, M., 1982. General ecological influence of the soil fauna on decomposition and nutrient circulation. *Oikos*, 3: 355–357.

MacLean, S.F. and Pitelka, F.A., 1971. Seasonal patterns of abundance of tundra arthropods near Barrow, Alaska. *Arctic*, 24: 19–40.

MacLean, S.F., Fitzerald, B.M. and Pitelka, F.A., 1974. Population cycles in arctic lemmings: winter reproduction and predation by weasels. *Arct. Alp. Res.*, 6: 1–12.

Madsen, J., 1988. Goose grazing in the Arctic. *Ibis*, 130(2): 302–303.

Malysheva, G.S., 1974. Ritmy sezonnogo razvitiya rastenyi listvenichnogo redkolesya v lesnom massive Ary-Mas (Taimyr) (Rhythms of plant seasonal development in Ary-Mas (Taymyr) forest island). In: V.N. Andreyev (Editor), *Biologicheskie problemy Severa*. Yakutsk, pp. 195–199.

Martin, Yu.L. and Piin, T.H., 1978. Flora napochvennykh lishainikov (Flora of soil surface lichens). In: B.N. Norin (Editor), *Ary-Mas. Prirodnye usloviya, flora i rastitelnost*. Nauka, Leningrad, pp. 101–123.

Matveyeva, N.V., 1968. Osobennosti struktury rastitelnosti osnovnykh tipov tundr v srednem techenii reki Pyasiny (Zapadnyi Taimyr) (Structure of main tundra types in the middle current of Pyasina river (western Taymyr)) (in Russian, with English summary). *Bot. Zh.*, 53(11): 1588–1603.

Matveyeva, N.V., 1971. Dinamika ottaivaniya merzloty v tundrakh zapadnogo Taimyra (Dynamics of thawing of the active soil layer in the tundras of western Taymyr) (in Russian, with English summary). In: B.A. Tikhomirov (Editor), *Biogeotsenozy taimyrskoi tundry i ikh produktivnost*. Nauka, Leningrad, pp. 45–56.

Matveyeva, N.V., 1979a. An annotated list of plants inhabiting sites of natural and anthropogenic disturbances of tundra cover in western Taymyr: the settlement Kresty. *Biol. Pap. Univ. Alaska*, 20: 18–29.

Matveyeva, N.V., 1979b. Flora i rastitelnost okrestnostei bukhty Marii Pronchishchevoi (severo-vostochnyi Taimyr) (Flora and vegetation in the vicinity of Maria Pronchishcheva bay (northeastern Taymyr). In: V.D. Aleksandrova and N.V. Matveyeva (Editors), *Arkticheskie tundry i polyarnye pustyni Taimyra*. Nauka, Leningrad, pp. 78–109.

Matveyeva, N.V., 1979c. Struktura rastitelnogo pokrova polyarnykh pustyn poluostrova Taimyr (mys Chelyuskin) (Structure of vegetation cover of Taymyr polar deserts (cape Chelyuskin)). *Ibis*, 5–27.

Matveyeva, N.V., 1980. Dve poezdki na ostrov Bolshoi Begichev (kratkyi ocherk flory i rastitelnosti) (Two trips to the Bolshoi Begichev island (a brief sketch of the flora and vegetation)) (in Russian, with English summary). *Bot. Zh.*, 65(11): 1543–1559.

Matveyeva, N.V., 1988a. Changes in tundra vegetation of Taimyr peninsula under man's impact. *Flora*, 180: 1–6.

Matveyeva, N.V., 1988b. The horizontal structure of tundra communities. In: H.J. During, M.J. Werger and J.H. Willems (Editors), *Diversity and Pattern in Plant Communities*, SPB Academic Publishing bv, The Hague, pp. 59–65.

Matveyeva, N.V., 1994. Floristic classification and ecology of tundra vegetation of the Taymyr Peninsula, northern Siberia. *J. Veg Sci.*, 5: 813–828.

Matveyeva, N.V. and Chernov, Yu.I., 1976. Polyarnye pustyni poluostrova Taimyr (Polar deserts of Taymyr) (in Russian,

with English summary) *Bot. Zh.*, 61(3): 297–312.

Matveyeva, N.V. and Chernov, Yu.I., 1977. Arkticheskie tundry na severovostoke poluostrova Taimyr, I (Arctic tundras at northeastern Taymyr) (in Russian, with English summary). *Bot. Zh.*, 62(7): 938–953.

Matveyeva, N.V and Zanokha, L.L., 1986. Rastitelnost Yuzhnykh tundr na zapadnom Tainyre (Vegetation of southern tundras at western Taymyr). In: Yu.I. Chernov and N.V. Matveyeva (Editors), *Yuzhnye tundry Taimyra*. Leningrad, pp. 5–67.

Matveyeva, N.V., Polozova, T.G., Blagodatskikh, L.S. and Dogostaiskaya, E.V., 1973. Kratkyi ocherk rastitelnosti okrestnostei Tainyrskogo biogeotsenologicheskogo stationara (A brief outline on the vegetation in the region of Taymyr biogeocenological station) In: B.A. Tikhomirov (Editor), *Biogeotsenozy taimyrskoi tundry i ikh produktivnost, 2*. Nauka, Leningrad, pp. 7–49.

Matveyeva, N.V., Parinkina, O.M. and Chernov, Yu I., 1975. Maria Pronchishcheva bay, USSR. In: T. Rosswall and O.W. Heal (Editors), *Structure and Function of Tundra Ecosystems (Ecol. Bull. (Stockholm)*, 20) pp. 61–72.

Medvedev, L.N. and Korotyaev, B.A., 1980. Ocherki po faune listoedov (Coleoptera, Chrysomelidae) arkticheskoi Azii i Kamchatki (Outlines on the leaf beetles (Coleoptera, Chrysomelidae) fauna of arctic Asia and Kamchatka). In: L.N. Medvedev (Editor), *Issledovaniya po entomofaune Severo-Vostoka SSSR*. Nauka OVO, Vladivostok, pp. 77–95.

Middendorf, A.F., 1869 *Puteshestvie na sever i vostok Sibiri, II (A Journey to the North and East of Siberia, II)* St. Petersburg, 310 pp.

Moskalenko, N.G., 1966. O krivykh tsveteniya nekotorykh tundrovykh fitotsenozov okrestnostei Norilska (On the blossoming curves of some tundra phytocenoses in the vicinity of Norilsk. *Byull. Mosk. O. Ispyt. Prir. Otd. Biol.*, 71(6): 128–135.

Moskalenko, N.G., 1970. K flore okrestnostei Norilska (severo-zapad Sredne-Sibirskogo plato) (On the flora of the vicinity of Norilsk (Northwest of Sredne-Sibirskoe plateau)) (in Russian, with English summary) *Bot. Zh.*, 55(2): 263–272.

Naumov, S.P., 1931. Mlekopitayushchie i ptitsy Gydanskogo poluostrova (Mammals and birds of Gydan peninsula). *Tr Polyarn. Kom. AN SSSR*, 4: 35–46.

Nikonov, V.V., 1985. Obshchie osobennosty pervichnoi biologicheskoi produktivnosti i biogeoklimaticheskikh tsiklov na Krainem Severe (na primere Kolskogo poluostrova) (General characteristics of the primary biological productivity and biogeocenological cycles in the Far North (with the Kola Peninsula as an example) (in Russian, with English summary). In: Yu.I. Chernov (Editor), *Soobshchestva Krainego Severa i chelovek*. Nauka, Moskva, pp. 79–90.

Nikolaeva, M.G., 1941. Kustarnikovyi tip rastitelnosti yuzhnoi chasti Bolshogo i Malogo Yamala (The shrub vegetation type in southern parts of Bolshoi and Malyi Yamal). *Bot. Zh.*, 26(1): 52–86.

Norin, B.N., 1979. *Struktura rastitelnykh soobshchestv vostochnoevropeiskoi lesotundry (Structure of Plant Communities of east-european forest tundra)*. Nauka, Leningrad, 200 pp.

Novichkova-Ivanova, L.N., 1963. Smeny sinuzyi pochvennykh vodoroslei Zemli Frantsa-Iosifa (Successional range of soil algae synusia on Franz Josef Archipelago) (in Russian, with English summary). *Bot. Zh.*, 48(1): 42–53.

Orlov, V.A., 1985. *Biologicheskie osobennosti lemmingov v tundrakh zapadnogo Taimyra (Biological Peculiarities of Lemmings in the Tundras of Western Taymyr)*. Avtoreferat diss., Moskva, 23 pp.

Orlov, V.A. and Sarancha, D.A., 1992. Matematicheskoe modelirovanie sistem "rastitelnost-lemmingi-pestsy" (Mathematical modeling of the systems "vegetation-lemmings-arctic foxes"). In: Yu.I. Chernov (Editor), *Tsenoticheskie vzaimodeistviya v tundrovykh ekosistemakh*. Nauka, Moskva, pp. 5–20.

Osmolovskaya, V.I., 1948. Ekologiya khishchnykh ptits poluostrova Yamal (Ecology of birds of prey of Yamal Peninsula). *Tr. Inst. Geogr. AN SSSR*, 41: 5–77.

Ovsyanikov, N.G. and Menyushina, I.E., 1986. Konkurentsiya iz-za korma mezhdu belymi sovami (*Nyctea scandiaca*) i pestsami (*Alopex lagopus*) (Competition for food between polar owls (*Nyctea scandiaca*) and arctic foxes (*Alopex lagopus*)). *Zool. Zh.*, 65(8): 901–910.

Pakarinen, D.V. and Vitt, D., 1974. The major organic components and caloric contents of high arctic bryophytes. *Can. J. Bot.*, 52(6): 1151–1161.

Panfilov, D.V., Shamurin, V.F. and Yurtsev, B.A., 1960. O sopryazhennom rasprostranenii shmelei i bobovykh v Arktike (On the joint distribution of bumblebees and legumes in Arctic). *Byull. Mosk. O Ispyt. Prir. Otd. Biol.*, 15(3): 53–62.

Parinkina, O.M., 1971. K mikrobiologicheskoi kharakteristike nekotorykh pochv zapadnogo Taimyra (Microbiological characteristics of certain soils on western Taymyr) (in Russian, with English summary). In: B.A. Tikhomirov (Editor), *Biogeotsenozy taimyrskoi tundry i ikh produktivnost*. Nauka, Leningrad, pp. 108–115.

Parinkina, O.M., 1973. Biologicheskaya produktivnost bakterialnykh soobshchestv tundrovoi zony (Biological productivity of bacterial communities in the tundra zone) (in Russian, with English summary) In: B.A. Tikhomirov (Editor), *Biogeotsenozy taimyrskoi tundry i ikh produktivnost, 2*. Nauka, Leningrad, pp. 58–76.

Parinkina, O.M., 1979a. K kharakteristike mikroflory pochv arkticheskikh tundr severo-vostochnoi chasti Taimyra (The characteristics of arctic tundra soil microflora of northeastern Taymyr). In: V.D. Aleksandrova and N.V. Matveyeva (Editors), *Arkticheskie tundry i polyarnye pustyni Taimyra*. Nauka, Leningrad, pp. 110–117.

Parinkina, O.M., 1979b. Mikroflora pochv polyarnykh pustyn mysa Chelyuskin (Soil microflora of polar deserts at cape Chelyuskin). *Ibis*, 28–34.

Parinkina, O.M., 1979c. Produktivnost mikroflory pochv Taimyra kak kriteryi ikh biologicheskoi aktivnosti (Productivity of microflora of Taymyr soils as a criterion of their biological activity). *Ibis*, 160–165.

Parinkina, O.M., 1986. Mikroorganismy v soobshchestvakh yuzhnykh tundr Taimyra (Microorganisms in Taymyr southern tundras). In: Yu.I. Chernov and N.V. Matveyeva (Editors). *Yuzhnye tundry Taimyra*. Nauka, Leningrad, pp. 151–168.

Parinkina, O.M., 1989. *Mikroflora tundrovykh pochv (Microflora of Tundra Soils)*. Nauka, Leningrad, 159 pp.

Parmusin, Yu.I., 1979. *Tundrolesje SSSR (Forest tundra of the USSR)*. Mysl, Moskva, 294 pp.

Pearson, O.P., 1966. The prey of carnivores during one cycle of mouse abundance. *J. Anim. Ecol.*, 35: 217–233.

Perel, T.S., Bulatova, N.Sh. and Viktorov, A.G., 1985. Khromosomnye rasy i areal *Eisenia atlavinytae* (Chromosome race

and area of *Eisenia atlavinytae*) *Dokl. AN SSSR*, 282(2): 499–500.

Peterson, H., 1982. Structure and size of soil animal populations. *Oikos*, 39(3): 306–329.

Petrovskyi, V.V., 1959. O strukture rastitelnykh assotsiatsyi valikovykh polygonalnykh bolot v nizovyakh r.Leny (Structure of plant associations of polygonal bogs in the low current of Lena river) (in Russian, with English summary). *Bot. Zh.*, 44(10: 1500–1507.

Petrovskyi, V.V., 1960. O strukturnykh elementakh fitotsenozov (On the structural elements of phytocenoses) (in Russian, with English summary). *Bot. Zh.*, 45(3). 382–393.

Petrovskyi, V.V., 1973. Spisok sosudistykh rastenyi o Vrangelya (List of vascular plants of Vrangel Island) (in Russian, with English summary). *Bot. Zh.*, 58(1) 113–126.

Petrovskyi, V.V., 1978. Geograficheskie svyazi flory ostrova Vrangelya (v svyazi s problemoi Beringyiskoi sushi) (Phytogeography of Vrangel island (in connection with the problem of Beringian land)) (in Russian, with English summary). *Bot. Zh.*, 63(5): 637–648.

Petrovskyi, V.V., 1985. Ocherk rastitelnosti ostrova Vrangelya (An outline of Vrangel island vegetation) (in Russian, with English summary). *Bot. Zh.*, 70(6): 742–751.

Pianka, E.R., 1983. *Evolutionary Ecology*, Second edition, Harper and Row Publishers, New York, Hagerstown, San Francisco, London, 416 pp.

Piin, T.H., 1979a. Napochvennye lishainiki mysa Chelyuskin (Terricolous lichens of cape Chelyuskin). In: V.D. Aleksandrova and N.V. Matveyeva (Editors), *Arkticheskie tundry i polyarnye pustyni Taimyra*. Nauka, Leningrad, pp. 61–73.

Piin, T.H., 1979b. Napochvennye lishainiki okrestnostei bukhty Marii Pronchishchevoi (severo-vostochnyi Taimyr) (Terricolous lichens in the environment of Maria Pronchishcheva Bay (northeastern Taymyr)). *Ibis*, 140–143.

Piin, T.H., 1984. Flora i rasprostranenie napochvennykh lishainikov yuzhnykh tundr Taimyra (Flora and distribution of terricolous lichens in the southern tundra of Taymyr) (in Russian, with English summary). In: Yu.L. Martin (Editor), *Flora i gruppirovki nizshikh rastenyi v prirodnykh i antropogennykh usloviyakh sredy*. Tallinn, pp. 134–172.

Piin, T.H. and Trass, H.H., 1971. Napochvennye lishainiki okrestnostei Tarei (Zapadnyi Taimyr) (Terricolous lichens in the vicinity of Tareya (western Taymyr) (in Russian, with English summary). In: B.A. Tikhomirov (Editor), *Biogeotsenozy taimyrskoi tundryi i ikh produktivnost*. Nauka, Leningrad, pp. 151–160.

Piin, T.H., Sdobnikova, N.B. and Parinkina, O.M., 1984. Nachalnye stadii zarastaniya pyaten gologo grunta v yuzhnykh tundrakh Taimyra (First stages of colonization of bare ground spots in the southern tundra of Taymyr) (in Russian, with English summary). In: Yu.L. Martin (Editor), *Flora i gruppirovki nizshikh rastenyi v prirodnykh i antropogennykh ekstremalnykh usloviyakh sredy*. Tallinn, pp. 20–49.

Piper, S.R., Maclean, S.F. and Christiansen, B., 1982. Enchytraeidae (Oligochaeta) from taiga and tundra habitats of north-eastern USSR. *Can. J. Zool.*, 60(11): 2594–2609.

Pitelka, F.A., Tomich, P.Q. and Treichel, G.W., 1955. Ecological relations of jaegers and owls as lemming predators near Barrow, Alaska. *Ecol. Monogr.*, 25: 85–117.

Pleske, Th., 1928. Birds of Eurasian tundra. *Mem. Boston Soc. Nat. Hist.*, 6(3): 1–485.

Polozova, T.G., 1970. Biologicheskie osobennosti *Eriophorum vaginatum* L. kak kochkoobrazovatelya (po nablyudeniyam v tundrakh zapadnogo Taimyra) (Biological peculiarities of *Eriophorum vaginatum* L. as a tussock forming plant (in western Taymyr tundras)) (in Russian, with English summary). *Bot. Zh.*, 55(3): 431–442.

Polozova, T.G., 1986. Vliyanie pozhara na rastitelnost gipoarkticheskikh yuzhnykh tundr na zapadnoi Chukotke (Fire influence on vegetation of western Chukotka hypoarctic southern tundras) (in Russian, with English summary). *Bot. Zh.*, 71(12): 1657–1663.

Polozova, T.G. and Boch, M.S., 1970. Osnovnye cherty fenologii rastenyi (Main features of plant phenology). In: B.N. Norin (Editor), *Ekologiya i biologiya rastenyi vostochnoevropeiskoi lesotundry*. Nauka, Leningrad, pp. 307–336.

Polozova, T.G. and Deyeva, N.M., 1978. Fenologicheskie nablyudeniya v osnovnykh rastitelnykh soobshchestvakh Taimyrskogo biogeotsenologicheskogo statsionara (Phenological observations in main plant communities in the vicinity of Taymyr biogeocenological station). In: B.A. Tikhomirov and B.A. Tomilin (Editors), *Struktura i funktsii biogeotsenozov taimyrskoi tundry*. Nauka, Leningrad, pp. 144–166.

Polozova, T.G. and Tikhomirov, B.A., 1971. Sosudistye rasteniya raiona Taimyrskogo statsionara (pravoberezhe Pyasiny bliz ustya Tarei, Zapadnyi Taimyr) (Vascular plants in the vicinity of Taymyr station (right Pyasina river bank near Tareya river mouth, western Taymyr)) (in Russian, with English summary). In: B.A. Tikhomirov (Editor), *Biogeotsenozy taimyrskoi tundry i ikh produktivnost*. Nauka, Leningrad, pp. 161–184.

Porsild, A.E., 1957. *Illustrated Flora of the Canadian Arctic Archipelago*. Bull. Nat. Mus., Canada, 209 pp.

Portenko, L.A., 1972, 1973. *Ptitsy Chukotskogo poluostrova i ostrova Vrangelya, 1, 2 (Birds of Chukotka peninsula and Vrangel island, 1, 2)*. Nauka, Leningrad, 324 pp.

Pospelova, E.V., 1972. Sezonnaya dinamika prirosta nekotorykh tundrovykh kustarnikov (Seasonal dynamics in the increment of some tundra shrubs). *Biol. Nauki*, 10: 66–70.

Ramenskaya, M.L., 1983. *Analiz flory Murmanskoi oblasti i Karelii (Analysis of Flora of the Murmansk District and Karelia)*. Nauka, Leningrad, 215 pp.

Ramenskyi, L.G., 1938. *Vvedenie v kompleksnoe pochvenno-geobotanicheskoe rationirovanie (Introduction to Soil-Vegetation Subdivision)*. Sel'khozgiz, Moskva, 620 pp.

Rebristaya, O.V., 1977. *Flora vostoka Bolshezemelskoi tundry (Flora of the Eastern Part of Bolshezemelskaya Tundra)*. Nauka, Leningrad, 334 pp.

Romanova, E.N., 1978. Micro- i mezoklimat Taimyra (Micro- and mesoclimates of Taymyr). In: B.A. Tikhomirov and B.A. Tomilin (Editors), *Struktura i funktsii biogeotsenozov taimyrskoi tundry*. Nauka, Leningrad, pp. 5–29.

Ryabchikov, A.M., 1972. *Struktura i dinamika geosfery, ee estestvennoe razvitie i izmenenie chelovekom (Structure and Dynamics of the Geosphere, its Natural Development and Changes under Impact by Man)*. Mysl, Moskva, 222 pp.

Safronova, I.N., 1979. Sosudistye rasteniya mysa Chelyuskin (Vascular plants of cape Chelyuskin). In: V.D. Aleksandrova and N.V. Matveyeva (Editors), *Arkticheskie tundry i polyarnye pustyni Taimyra*. Nauka, Leningrad, pp. 50–53.

Sambuk, F.V., 1937. O klassifikatsii rastitelnosti tundrovoi zony. (On the classification of the tundra vegetation zone). *Sov. Bot.*, 2: 34–51.

Sambuk, F.V. and Dedov, A.A., 1934. Podzony propechorskikh tundr (The tundra subzones in the region of Pechera river). *Tr. Bot. Inst. AN SSSR*, 3, 1: 29–52.

Savchenko, E.N., 1969. Sem. Tipulidae-dolgonozhki (Fam. Tipulidae-crane flies). In: A.A. Shtakelberg (Editor), *Opredelitel nasekomykh evropeiskoi chasti SSSR, V, 1*. Nauka, Leningrad, pp. 59–86.

Schalow, H., 1904. Die Vogel der Arktis. *Fauna Arctica, 4*. Verlag Fischer, Jena, pp. 79-288.

Schrenk, A., 1848, 1854. *Puteshestvie k Severo-vostoku Evropeiskoi Rossii cherez tundry samoedov k severnym Uralskim goram predprinyatoe v 1837 godu (A Journey to the Northeast of the European Part of Russia through the Samojed Tundra to Northern Ural Mountains, undertaken in 1837)*. Bd. 1, 2. St. Petersburg, 665 pp.

Sdobnikov, V.M., 1937. Raspredelenie mlekopitayushchikh i ptits po tiparm mestoobitanyi v Bolshezemelskoi tundre i na Yamale (Distribution of birds and mammals in the environmental types in Bolshezemelskaya tundra and Yamal). *Tr Arkt. Inst.*, 63: 82–97.

Sdobnikov, V.M., 1959. Biotopy severnogo Taimyra i plotnost populyatsii naselyayushchikh ikh zhivotnykh (Biotopes of northern Taymyr and the population density of animals inhabiting them) (in Russian, with English summary). *Zool. Zh.*, 38(2): 243–252.

Sdobnikova, N.V., 1986. Pochvennye vodorosli v yuzhnykh tundrakh Taimyra (Soil algae in southern tundras of Taymyr). In: Yu.I. Chernov and N.V. Matveyeva (Editors). *Yuzhnye tundry Taimyra*. Nauka, Leningrad, pp. 68–79.

Semenov-Tyan-Shanskyi, O.I., 1977. *Severnyi olen (Northern reindeer)*. Nauka, Moskva, 94 pp.

Serebryakov, I.G., 1961. Ritm sezonnogo razvitiya rastenyi Khibinskikh gor (Rhythm of seasonal plant development of Khibini mountains). *Byull. Mosk. O. Ispyt. Prir. Otd Biol.*, 66(5): 78–97.

Serebryakov, I.G., 1963. Nekotorye dannye o ritme sezonnogo razvitiya rastenyi dolny reki Pyasiny v ee nizhnem techenii (Some data on the seasonal development of plants in the low current of Pyasina river). *Byull. Mosk. O. Ispyt. Prir. Otd Biol.*, 68(2): 77–90.

Serebryakov, I.G., 1964. Sravnitelnyi analiz nekotorykh priznakov ritma sezonnogo razvitiya rastenyi razlichnykh botaniko-geograficheskikh zon SSSR (A comparative analysis of some features of seasonal development of plants in various botanical-geographical zones of the USSR). *Byull. Mosk. O. Ispyt. Prir. Otd. Biol.*, 64(5): 62–75.

Severin, S., 1909. Bakterialnoe naselenie pochv iz dalekogo Severa (Bacterial populations of soils from the far North). *Vestn. Bakt. Agron. Stn.*, 15: 116–128.

Shamurin, V.F., 1956. Voprosy opyleniya u rastenyi (Problems of plant pollination) (in Russian, with English summary). *Bot. Zh.*, 44(9): 1380–1384.

Shamurin, V.F., 1957. Sezonnyi rutm i ekologiya tsveteniya rastenyi c raione bukhty Tiksi (Seasonal rhythm and ecology of plant flowering in the environment of Tiksi bay). *Tr. Fenologicheskogo soveshchaniya*. Leningrad, pp. 279–289.

Shamurin, V.F., 1962 O ponyatii "aspekt" i smene aspektov v tundrovykh tsenozakh (On the concept "aspect" and change of aspects in tundra cenoses). *Probl. Bot.*, 1(6): 198–207.

Shamurin, V.F., 1966a. Rol nasekomykh opylitelei v tundrovykh soobshchestvakh (Role of insect pollinators in tundra communities). In: A.G. Voronov (Editor), *Organizmy i prirodnaya sreda. (Voprosy geografii, 69)*, Moskva, pp. 98–117.

Shamurin, V.F, 1966b. Sezonnyi ritm i ekologiya tsveteniya rastenyi tundrovykh soobshchestv na severe Yakutii (Seasonal rhythm and ecology of flowering of tundra plants in northern Yakutia). *Rastit. Krainego Sev. Ee Osvoenie*, 8. Izd. AN SSSR, pp. 5–125.

Shamurin, V.F., Tikhmenev, E.A. and Levkovskyi, V.P., 1974. Sutochnyi ritm tsveteniya v svyazi s problemoi adaptatsii rastenyi k usloviyam Arktiki (Diurnal rhythm of flowering in connection with the problem of plant adaptation to arctic environments). In: V.N. Andreyev (Editor), *Biologicheskie problemy Severa, 3. Botanika i rastitelnye resursy*. Yakutsk, pp. 184–187.

Sharova, I.Kh., 1981. *Zhiznennye formy zhuzhelits (Coleoptera, Carabidae) (Life Forms of Ground Beetles (Coleoptera, Carabidae))*. Nauka, Moskva, 360 pp.

Shelford, V.E., 1943. The abundance of the collared lemming (*Dicrostonyx groenlandicus*) in the Churchill Area, 1929–1940. *Ecology*, 24: 472–484.

Shvetsova, V.M. and Voznesenskyi, V.L., 1970. Sutochnye i sezonnye izmeneniya intensivnosti fotosinteza u nekotorykh rastenyi Zapadnogo Taimyra (Diurnal and seasonal changes in photosynthetic intensity of certain plants, at western Taymyr) (in Russian, with English summary). *Bot. Zh.*, 55(1): 66–76.

Shwarts, S.S., 1963. *Puti prisposobleniya nazemnykh pozvonochnykh zhivotnykh k usloviyam sushchestvovaniya v Subarktike, 1. Mlekopitayushchie (Adaptations of Terrestrial Vertebrate Animals to the Existence in Subarctic, 1 Mammals)*. Sverdlovsk, 131 pp.

Sochava, V.B., 1934. Rastitelnye assotsiatsii Anabarskoi tundry (Plant associations of Anabar tundra). *Bot. Zh.*, 19(3) 543–551.

Stebayev, I.V., 1959. Pochvennye bespozvonochnye salekhardskikh tundr i izmeneniya ikh gruppirovok pod vliyaniem zemledeliya (Complexes of soil invertebrates in Salekhard tundras and their changes under agricultural influence) (in Russian, with English summary). *Zool. Zh.*, 38(10): 1559–1572.

Stepanova, I.V. and Tomilin, B.A., 1971. Griby-mikromitsety Taimyrskogo statsionara (Micromycetes of Taymyr station) (in Russian, with English summary). In: B.A. Tikhomirov (Editor), *Biogeotsenozy taimyrskoi tundry i ikh produktivnost*. Nauka, Leningrad, pp. 138–144.

Stepanova, I.V. and Tomilin, B.A., 1978. Griby-mikromitsety Taimyrskogo statsionara, 2 (Micromycetes of Taymyr station, 2). In: B.A. Tikhomirov and B.A. Tomilin (Editors), *Struktura i funktsii biogeotsenozov Taimyrskoi tundry*. Nauka, Leningrad, pp. 217–227.

Stepanova, I.V. and Tomilin, B.A., 1980 Griby-komponenty tundrovykh biogeotsenozov (Fungi as a component of tundra biogeocenoses). In: B.A Tomilin (Editor). *Biogeotsenozy Taimyrskoi tundry*. Nauka, Leningrad, pp. 165–192.

Stepanyan, L.S., 1975. *Sostav i raspredelenie ptits fauny SSSR. Nevorobjinye (Composition and Distribution of the Bird Fauna of USSR. Non-Passermes)*. Nauka, Moskva, 369 pp.

Stepanyan, L.S., 1978. *Sostav i raspredelenie ptits fauny SSSR. Vorobjinye (Composition and Distribution of the Bird Fauna of USSR. Passerines)*. Nauka, Moskva, 170 pp.

Stepanyan, L.S., 1983. *Podvidy i vidy-dvoiniki v avifaune SSSR (Subspecies and Double Species in Avifauna of USSR)*. Nauka, Moskva, 293 pp.

Stishov, M.S., Chernov, Yu.I. and Vronskyi, N.V., 1989. Fauna i naselenie ptits podzony arkticheskikh tundr (Fauna and bird population in the arctic tundra subzone). In: Yu.I. Chernov (Editor), *Ptitsy v soobshchestvakh tundrovoi zony*. Nauka, Moskva, pp. 5–39.

Striganova, B.R., 1982. Pishchevye svyazi pochvennykh lichinok komarovdolgonozhek (Diptera, Tipulidae) v arkticheskikh tundrakh (Trophic relations of soil larvae of crane flies (Diptera, Tipulidae) in arctic tundras) (in Russian, with English summary). *Zool. Zh.*, 61(4) 535–541.

Striganova, B.R., 1985. Pitanie dozhdevykh chervei *Eisenia nordenskioldi* v Subarktike (The food of earthworms *Eisenia nordenskioldi* in the Subarctic). *Dokl. Akad Nauk SSSR*, 284(1): 253–256.

Striganova, B.R. and Chernov, Yu.I., 1981. Troficheskie otnosheniya pochvennykh zhivotnykh i ikh zonalno-landshaftnye osobennosti (Trophic relations of soil animals and their zonal landscape peculiarities). In: M.S. Gilyarov (Editor), *Strukturno-funktsionalnaya organizatsiya biogeotsenozov*. Nauka, Moskva, pp. 269–288.

Sumina, O.I., 1994. Plant communities on anthropogenically disturbed sites on the Chutkotka Peninsula, Russia. *J. Veg. Sci.* 5: 885–896.

Sushkina, N.N., 1960. Ob osobennostyakh mikroflory arkticheskikh pochv (On the peculiarities of microflora of arctic soils). *Pochvovedenie*, 4: 57–67.

Svatkov, N.N., 1970. Ostrov Vrangelya (Vrangel Island). In: I.P. Gerasimov (Editor), *Sovetskaya Arktika*. Nauka, pp. 453–472.

Syroechkovskyi, E.E., 1986. *Severnyi olen (Northern reindeer)*. Agropromizdat, Moskva. 94 pp.

Syroechkovskyi, E.V., 1978. Rasmery lebedei, gusei i kazarok v svyazi s adaptatsiei k polyarnym usloviyam (Size of swans, geese (*Anser* and *Branta*) in connection with adaptation to polar conditions) (in Russian, with English summary). *Zool. Zh.*, 57(5): 738–749.

Tieszen, L.L., Miller, P.C. and Oechel, W.C., 1980. Photosynthesis. In: J. Brown, P.C. Miller, L.L. Tieszen and F.L. Bunnell (Editors), *An Arctic Ecosystem (The Coastal Tundra at Barrow, Alaska)*. Dowden, Hatchinson & Ross, Inc., Stroudsburg, PA, pp. 102–139.

Tikhmenev, E.A., 1976. Autekologiya rastenyi ostrova Vrangelya (Autecology of plants of Vrangel Island) (in Russian, with English summary). *Bot. Zh.*, 61(2): 164–176.

Tikhmenev, E.A. and Levkovskyi, V.P., 1973. K autekologii zlakov arkticheskoi tundry ostrova Vrangelya (On the autecology of grasses in arctic tundra of Vrangel Island) (in Russian, with English summary). *Bot. Zh.*, 58(10): 1474–1484.

Tikhomirov, B.A., 1946. K proiskhozhdeniyu lugovogo tipa rastitelnosti v Arkticheskoi Evrasii (On the origin of meadow vegetation types in Arctic Eurasia). In: B.K. Shishkin and V.S. Sokolov (Editors), *Sbornik nauchnykh trudov Botanicheskogo Instituta AN SSSR*, pp. 157–182.

Tikhomirov, B.A., 1952. Znachenie mokhovogo pokrova v zhizni rastenyi Krainego Severa (Role of moss cover in plant life of the Far North). *Bot. Zh.*, 37(5): 629–638.

Tikhomirov, B.A., 1957. Dinamicheskie yavleniya v rastitelnosti pyatnistykh tundr Arktiki (Dynamic phenomena in vegetation of arctic frost-boil tundras). *Bot. Zh.*, 42(1): 1691–1717.

Tikhomirov, B.A., 1959. *Vzaimosvyazi zhivotnogo mira i rastitelnogo pokrova tundry (Interrelations between Animals and Vegetation in Tundra)*. Izd. AN SSSR, Moskva-Leningrad, 103 pp.

Tikhomirov, B.A., 1960. Vliyanie suslika dlinnokhvostogo (*Citellus undulatus*) na floru i rastitelnost Chukotskoi tundry (The influence of souslik (*Citellus undulatus*) on flora and vegetation of Chukotka tundra). In: T.A. Rabotnov (Editor), *Sbornik rabot po geobotanike, botanicheskoi geografii, sistematike rastenyi i paleogeografii*. Izd. AN SSSR, Moskva, pp. 277–290.

Tikhomirov, B.A., 1963. *Ocherki po biologii rastenyi Arktiki (Outlines on Biology of Arctic Plants)*. Izd. AN SSSR, Moskva-Leningrad, 153 pp.

Tishkov, A.A., 1977. Vzaimodeistvie zhivotnykh fitofagov s rastitelnostyu tundry (Interrelations between phytophagous animals and tundra vegetation) (in Russian, with English summary). *Zh. Obsheh. Biol.*, 38(1): 15–23.

Tishkov, A.A., 1985a. Pervichnye suktsessii v arkticheskikh tundrakh zapadnogo poberezhya Spitsbergena (Svalbard) (Primary succession in arctic tundras of the western coast of Spitsbergen (Svalbard)). *Izv. AN SSSR*, 3: 99–105.

Tishkov, A.A., 1985b. Rastitelnoyadnye mlekopitayushchie v ekosistemakh tundr (Herbivorous mammals in tundra ecosystems). In: V.E. Sokolov and G.V. Kuznetsov (Editors), *Mlekopitayushchie v nazemnykh ekosistemakh*. Nauka, Moskva, pp. 38–66.

Tolmachev, A.I., 1930. O proiskhozhdenii flory Vaigacha i Novoi Zemli (On the origin of flora of Vaigach and Novaya Zemlya). *Tr. Bot. Muz. AN SSSR*, 22: 181–205.

Tolmachev, A.I., 1931. Materialy dlya flory evropeiskikh arkticheskikh ostrovov (Data for flora of the European arctic islands). *Zh. Russ. Bot. O.*, 31(5–6): 459–472.

Tolmachev, A.I., 1986. *Metody sravnitelnoi floristiki i problemy florogeneza (Methods of Comparative Floristics and Problems of Florogenesis)*. Nauka SO, Novosibirsk, 196 pp.

Tomilin, B.A., 1971. Nekotorye svedeniya o geograficheskom rasprostranenii i ekologii gribov Taimyrskogo statsionara (Some data on geographical distribution and ecology of fungi in the vicinity of Taymyr station). In: B.A. Tikhomirov (Editor), *Biogeotsenozy taimyrskoi tundry i ikh produktivnost*. Nauka, Leningrad, pp. 130–137.

Tomkovich, P.S. and Vronskyi, N.V., 1988. Fauna ptits okrestnostei Diksona (Bird fauna in the vicinity of Dikson). *Sb. Tr. Zool. Muz. MGU*, 16: 39–77.

Tugarinov, A.Ya., 1929. O proiskhozhdenii arkticheskoi fauny (On the origin of arctic fauna). *Priroda*, pp. 7–8.

Tyrtikov, A.P., 1974. *Vliyanie rastitelnogo pokrova na promerzanie i protaivanie gruntov (Influence of Vegetation Cover on Soil Freezing and Thawing)*. Izd. MGU, Moskva, 135 pp.

Tyrtikov, A.P., 1979. *Dinamika rastitelnogo pokrova i razvitie merzlotnykh form reljefa (Dynamics of the Plant Cover and the Development of Permafrost Relief Forms)*. Nauka, Moskva, 116 pp.

Uspenskyi, S.M., 1956. *Ptichi bazary Novoi Zemli (Bird Colonies on Novaya Zemlya)*. Izd. AN SSSR, Moskva, 180 pp.

Uspenskyi, S.M., 1969. *Zhizn v vysokikh shirotakh. Na primere ptits (Life at high latitudes. With birds as an example)*. Mysl, Moskva, 463 pp.

Vargina, N.E., 1978. Flora sosudistykh rastenyi (Vascular plant flora). In: B.N. Norin (Editor), *Ary-Mas. Prirodnye usloviya, flora i rastitelnost*. Nauka, Lemngrad, pp. 65–86.

Vasilevskaya, V.D., 1980. *Pochvoobrazovanie v tundrakh Sred-*

nei Sibiri (The Soil Formation in the Tundras of Middle Siberia). Nauka, Moskva. 233 pp.

Vasilkov, B.P., 1967. O gribakh (makromitstakh) Sovetskoi Arktiki (On fungi (macromycetes) of Soviet Arctic). *Mikol. Fitopatol.*, 1(1): 17–25.

Vasilkov, B.P., 1969. Sumchatye griby (makromitsety) Sovetskoi Arktiki (Macromycetes of Soviet Arctic) *Mikol. Fitopatol.*, 3(2): 114–120.

Vilchek, G.E., 1986. Produktivnost nekotorykh fitotsenozov Vorkutinskikh tundr (Productivity of some Vorkuta tundras). *Ekologiya*, 2: 8–13.

Vilchek, G.E., 1987. Produktivnost tipichnykh tundr Taimyra (Productivity of typical tundras of Taymyr). *Ekologiya*, 5: 38–43.

Vinogradova, A.N., 1937. Geobotanicheskyi ocherk olenjikh pastbishch raiona reki Pyasiny (Geobotanical description of reindeer pastures in Pyasina river area). *Tr. Arkt. Inst.*, 63: 5–45

Vinokurov, A.A., 1971. Fauna pozvonochnykh zhivotnykh raiona Taimyrskogo statsionara (Zapadnyi Taimyr) (Vertebrate fauna in the vicinity of Taymyr station (western Taymyr)) (in Russian, with English summary). In: B.A. Tikhomirov (Editor), *Biogeotsenozy Taimyrskoi tundry i ikh produktivnost*. Nauka, Leningrad, pp. 212–231.

Vinokurov, N.N., 1979. *Nasekomye poluzhestkokrylye (Heteroptera) Yakutii (Heteropteran insects (Heteroptera) in Yakutia)*. Nauka, Leningrad. 232 pp.

Vital, A.D., 1978. Sezonnaya dinamika prirosta arkticheskikh rastenyi po nablyudeniyam na zapadnom Taimyre (Seasonal dynamics of arctic plant growth at western Taymyr) In: B.A. Tikhomirov and B.A. Tomilin (Editors), *Struktura i funktsii biogeotsenozov Taimyrskoi tundry*. Nauka, Leningrad, pp. 58–71.

Vital, A.D., 1980. O svyazi lineinykh prirostov pobegov i listjev arkticheskikh rastenyi s khodom temperatury i ritmom fenologicheskogo razvitiya (On the correlation of linear increase of shoots and leaves with temperature and phenological rhythm. In: B.A. Tomilin (Editor), *Biogeotsenozy Taimyrskoi tundry*. Nauka, Leningrad, pp. 97–104.

Vronskyi, N.V., 1986. Materialy k avifaune severo-zapadnogo Taimyra (Data on avifauna of northwestern Taymyr). In: E.E. Syroechkovskyi (Editor), *Fauna i ekologiya ptits i mlekopitayushychikh Srednei Sibiri*. Nauka, Moskva, pp 51–61.

Vronskyi, N.V., 1987. K avifaune severo-zapadnogo Taimyra (On avifauna of northwestern Taymyr). In: E.E. Syroechkovskyi (Editor), *Fauna i ekologiya ptits Srednei Sibiri*. Nauka, Moskva, pp. 28–38.

Vysotskyi, 1909. O fitotopologiqeskikh kartakh, sposobakh ikh sostavlenya i ikh prakticheskoe znachenie (Phytotopological maps, their drawing and their meaning for practice). *Pochvovedenie*, 1(2): 97–124.

Washburn, A.L., 1956. Classification of patterned ground and review of suggested origin. *Geol. Soc.*, 67: 823–866.

Whittaker, J.B., 1974. Interactions between fauna and microflora at tundra sites. In: A.J. Holding, O.W. Heal and S.F. MacLean (Editors), *Soil Organisms and Decomposition in Tundra*. Tundra Biome Steering Comittee, Stockholm, Sweden, pp. 183–196.

Whittaker, R.H., 1965 Dominance in land plant communities. *Science*, 147: 250–260.

Whittaker, R.H., 1977. Evolution of species diversity in land communities. *Evol. Biol.*, 10: 1–67.

Wielgolaski, F.E., 1986. Production-ecology and functioning of polar and alpine ecosystems. In: N. Polunin (Editor). *Ecosystem Theory and Evaluation*. John Wiley & Son, pp. 12–34.

Wielgolaski, F.E., 1990. Zavisimost pervichnoi produktivnosti ot klimaticheskikh i edaficheskikh faktorov (The dependence of the primary productivity on climate and edaphic factors). *Bot. Zh.*, 75(2): 203–206.

Wiggins, I.L. and Thomas, J.H., 1962. *A Flora of Alaskan Arctic Slopes*. Arctic Institute of North America, Special publication N4, 425 pp.

Williams, J.B. and Batzli, G.O., 1982. Pollination and dispersion of five species of lousewort (*Pedicularis*) near Atkasson, Alaska, USA. *Arct. Alp. Res.*, 14: 59–74.

Yakobson, G.G., 1905–1916. *Zhuki Rossii i Zapadnoi Evropy (Beetles of Russia and Western Europe)*. Moskva, 1024 pp.

Yudin, B.S., Krivosheev, V.G. and Belyaev, V.G., 1976. *Melkie mlekopitayushchie severa Dalnego Vostoka (Small Mammals of the North of the Far East)*. Nauka SO, Novosibirsk, 269 pp.

Yurtsev, B.A., 1966 *Gypoarkticheskyi botaniko-geograficheskyi poyas i proiskhozhdenie ego flory (The Hypoarctic Botanical-Geographical Belt and the Origin of its Flora)* Nauka, Moskva-Leningrad, 94 pp.

Yurtsev, B.A., 1974. *Problemy botanicheskoi geografii Severo-Vostochnoi Azii (The Problems of Botanical Geography of North-East Asia)*. Nauka, Leningrad, 160 pp.

Yurtsev, B.A., 1986. Rol istoricheskogo faktora v osvoenii rasteniyami ekstremalnykh uslovyi Arktiki (Role of the historical factor in settling of extreme arctic environments). In V.E. Sokolov, Yu.I. Chernov and B.Ya. Vilenkin (Editors), *Organismy, populyatsii i soobshchestva v ekstremalnykh usloviyakh*. Nauka, Moskva, pp. 146–148.

Yurtsev, B.A. and Korobkov, A.A., 1979. An annotated list of plants inhabiting sites of natural and anthropogenic disturbances of tundra cover: southeasternmost Chukotka peninsula. *Biol. Pap. Univ. Alaska*, 20: 1–17.

Yurtsev, B.A., Tolmachev, A.I. and Rebristaya, O.V., 1978. Floristicheskoe ogranichenie i razdelenie Arktiki (The floristical delimination and subdivision of the Arctic). In: B.A. Yurtsev (Editor), *Arkticheskaya floristicheskaya oblast*. Nauka, Leningrad, pp. 9–104.

Zanokha, L.L., 1986. Sezonnaya dinamika rastitelnykh soobshchestv v podzone yuzhnykh tundr Taimyra (Seasonal dynamics of plant communities in the southern tundra subzone of Taymyr). In: Yu.I. Chernov and N.V. Matveyeva (Editors), *Yuzhnye tundry Taimyra*. Nauka, Leningrad, pp. 135–150.

Zanokha, L.L., 1993. Klassifikatsiya lugovykh soobshchestv tundrovoi zony poluostrova Taymyr: assotsiatsiya Pediculari verticillatae-Astragaletum arctici (Classification of meadow communities of the tundra zone in Taymyr Peninsula: association *Pediculari verticillatae-Astragaletum arctici*) (in Russian, with English summary). *Bot. Zh.*, 78(3): 110–121.

Zanokha, L.L., 1995. Klassifikatsiya lugovykh soobshchestv tundrovoi zony poluostrova Taymyr: assotsiatsiya Saxifrago hirculi-Poetum alpigenae (Classification of meadow communities of the tundra zone in Taymyr Peninsula: association *Saxifrago hirculi-Poetum alpigenae*) (in Russian, with English summary). *Bot. Zh.*, 80(5): 25–35.

Zaslavskaya (Koroleva), T.M., 1982. Izuchenie flory Anyuiskogo nagorya (zapadnaya Chukotka) (Study of the flora at Anyui plateau (western Chukotka) (in Russian, with English summary). *Bot. Zh.*, 67(2): 185–195.

Zhukova, A.L., 1973. Vidovoi sostav i raspredelenie pechenochnykh mkhov v rastitelnykh soobshchestvakh raiona taimyrskogo statsionara (Composition and distribution of liverworts in plant communities in the vicinity of the Taymyr station). In: B.A. Tikhomirov (Editor). *Biogeotsenozy taimyrskoi tundry i ikh produktivnost, 2*. Nauka, Lenngrad, pp. 120–127.

Zhukova, A.L., 1978. Flora pechenochnykh mkhov (Liverwort flora). In: B.N. Norin (Editor), *Ary-Mas. Prirodnye usloviya, flora i rastelnost*. Nauka, Leningrad, pp. 91–101.

Zhukova, A.L., 1986. Pechenochnye mkhi okrestnostei pos. Kresty (podzona yuzhnykh tundr, zapadnyi Taimyr) (Liverworts in the vicinity of Kresty settlement (southern tundra subzone, western Taymyr)). In: Yu.I. Chernov and N.V. Matveyeva (Editors), *Yuzhnye tundry Taimyra*. Nauka, Leningrad, pp. 80–88.

Zubkov, A.I., 1934. O vegetatsionnom periode v Arktike (On the vegetation period in Arctic). *Byull. Arkt. Inst.*, 3: 17–21.

Zubkov, A.I., 1935. Prodolzhitelnost vegetatsionnogo perioda na Severnom ostrove Novoi Zemli (The duration of vegetation period on northern island of Novaya Zemlya). *Arktika*, 3: 14–20.