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ECOLOGICAL ASPECTS OF VERTICAL DIFFERENTIATION OF THE PLANT COVER IN HIGH BOREAL MOUNTAINS

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The concept of a close association between vertical differentiation of the plant cover and the zonal position of certain mountainous regions or groups of mountainous regions is substantiated. Patterns in vegetation belt structure in high boreal mountains are described with special attention to the characteristics of the belt of cold bald-peak deserts.

The ideas on the zonal and belt-like distribution of vegetation, soil, and animals were first expressed by von Humboldt (1817), and subsequently developed in the works of V. V. Dokuchaev (1899), L. S. Berg (1947, 1952), and other investigators. The belt-like distribution of natural elements in mountains was at first described as "vertical zonality." The similarity or at least analogy between "vertical" and "horizontal" zones was emphasized. Later, as facts accumulated, it became apparent that elements of vertical and horizontal differentiation of the plant cover were not totally analogous, because of which the term "belts" began to be used preferentially to describe the vertical distribution of vegetation in mountains. Nevertheless, some investigators even now continue to use the term "vertical zonality."

BASIC REASONS FOR SEPARATING MOUNTAIN VEGETATION INTO ALTITUDINAL BELTS

It must be emphasized that since the formulation and development of theories on vertical zonality landscape and ecological ideas have been incorporated into the concept of "belt" or "vertical zone." Regardless of the scientific specialization of investigators, all of them, whether geographers, botanists or climatologists, described a belt not by some similar attribute (e.g., flora or vegetation), but by an aggregate of interrelated natural components (soil, climate, plants and animals); i.e., they approached this concept from an ecological (biogeocenological) standpoint.

Scientific theories on the belt structure of vegetation were based to a great extent on data for the Alps in Central Europe. Terms such as "subalpine" and "alpine" belt were coined and first used here (Christ, 1879; Brockmann-Jerosch, 1929; Schröter, 1926). At present it is customary to distinguish altitudinal belts in the Alps: hill, piedmont (submontane), mountainous (montane), subalpine, alpine, and nival ("La vegetation et la faune des Alpes," 1970).

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Investigators visiting other mountainous regions on Earth very naturally attempted to compare the patterns they found in the altidudinal distribution of vegetation with the classic column of belts in the Alps and initially used "alpine" nomenclature for belts. The terms "subalpine" and "alpine" belts began to be used to describe mountain vegetation of mountainous regions not at all similar to the Alps, such as volcano peaks in Japan and high mountains in tropical Africa and South America.

Nevertheless, as knowledge on mountain vegetation from different regions of the world accumulated, the inappropriateness of the "alpine template" for many mountain masses outside of Central Europe became obvious. In his exceptionally important and interesting article, A. I. Tolmachev (1948) convincingly showed that it is necessary to distinguish at least six basic types of mountainous landscapes:

1) Alpine, characteristic in its typical form of the Alps, Caucasus, the Altai (in part), central and eastern Tien Shan (especially its northern range), and mountains at the eastern boundary of Central Asia;

2) bald-peak (mountain tundra or "goltsy"), associated with mountain peaks in Siberia and the Far East;

3) highland xerophytic, typical for southern Central Asia, Afghanistan, Iran, Asia Minor, the Armenian highlands, northwest Africa, southern Spain, Sicily, and the Balkan peninsula;

4) paramo, typical for mountains in South America (northern region) and Equatorial Africa;

5) mountain-steppe;

6) mountain-desert (the last two are typical for regions of highland Asia with a sharply continental climate, for example, Pamir or Tibet).

Not only was the well-known analogy between altidudinal belts and zonal subdivisions of plants in lowlands demonstrated in subsequent works, but the dependence of vegetation belts on the zonal position of a certain mountainous region or its areas was discovered (Stanyukovich, 1973; Gorchakovskii, 1965, 1975).

It may be stated on the basis of these theories that the nature of vegetation at upper altitudes of some mountainous region depends greatly on its position within the system of horizontal zonality, and also on the altitude of the mountains. Each landscape zone (boreal, nemoral, subtropical, tropical, arid, etc.) has its own spectrum of altitudinal belts of vegetation. The classic "alpine" type of belt structure is represented only by the nemoral (broad-leaved forest) zone. The terms "alpine belt," subalpine belt," and others are suitable for describing vegetation and ecosystems in the Alps and some other mountains with similar ecological conditions (e.g., humid region of the Caucasus), but are totally inappropriate for vegetation and ecosystems in Africa, South America, and boreal and arid zones of Eurasia.

Another column, different from the Alps, of altitudinal belts can be traced in the boreal (coniferous forest, taiga) zone; "subpeak" and mountain-tundra belts and the belt of cold bald-peak deserts have evolved here in the high mountains (Gorchakovskii, 1975). Mountain plant belts in the boreal zone differ sharply in climatic, soil, floristic, and phytocenological criteria from mountain belts in the nemoral zone; therefore, the "alpine" nomenclature cannot be used here.

DIFFERENT APPROACHES TO THE DEMARCATION AND NOMENCLATURE OF ALTITUDINAL BELTS OF VEGETATION

Despite the considerable progress in accumulating information on mountain ecosystems and their plant components, some investigators continue to apply the "alpine template" of belts to mountainous regions whose landscapes differ sharply from the alpine, or they employ a "vague" terminology for belts without any landscape, biogeographic, or plant geographic value. In demarcating belt boundaries, greater significance is sometimes attached to geomorphological and morphometric parameters than to biochorological aspects.

Noteworthy in this regard is the article by P. Plesnik (1977), who emphasizes that vertical differentiation of vegetation is closely related to landscape structure. Nevertheless, he believes that the nomenclature for vegetation belts should not coincide with that for landscape belts. In his opinion, vertical belts should reflect the general patterns in global plant distribution and be described in terms based on vegetation features (e.g., belts of hard-leaved, coniferous, mixed aestival forests). Nonetheless, since vegetation is a major component of ecosystems and the landscapes they comprise, belts of vegetation often coincide in practice with landscape belts.

Vagueness in the naming of belts (lower, middle, upper) or names based on relief features (hilly belt, piedmont belt, etc.) cannot satisfy the biogeographer and ecologist. An example is the upper, middle, and lower oroboreal altitudinal belts defined by L. Khamet-Akhti (1976). Likewise unsuccessful are the attempts of some investigators (Khamet-Akhti, 1979) to develop a unified terminology for vertical differentiation of plants in the northern and southern hemispheres. As E. M. Lavrenko (1964)* notes with good reason, the typology of vegetation belts in mountains should be coordinated with general global plant geographic patterns, in part, with the division of continents into large plant geographic districts — dominions, regions, and provinces, and in several cases into zones and subzones of vegetation.

L. I. Malyshev (1977) rather recently assumed the role of an apologist for out-of-date theories on vegetation belts in mountains. Without providing any convincing conclusions and ignoring the scientific data accumulated, he proposes to demarcate the "classic" alpine and subalpine belts in the mountains of northern Asia, and does not differentiate the belt of cold bald-peak deserts but combines it with the alpine, since it differs from the lower belt only in "negative features" and has no unique species of flowering plants. Such statements do not withstand serious criticism. First of all, we must recall that high boreal mountains of northern Asia do not have plant communities typical for the alpine belt in Central Europe, namely the low-grass alpine meadows ("carpets," "flower beds"); mountain tundras are found here instead. The mountain-tundra belt differs from the alpine in several major features, as has been demonstrated in the work of one of this article's authors (Gorchakovskii, 1975). The status of the belt of cold bald-peak deserts deserves to be discussed more extensively.

FEATURES OF THE BELT OF COLD BALD-PARK DESERTS

The belt of cold bald-peak deserts generally occupies the highest mountain levels in high boreal mountains. Environmental conditions here are very harsh. Hurricane-force winds with severe snowstorms are common in winter. Winds do not have just a desiccating and corrosive effect on plants; they are also responsible for the minimal snow cover and the absence of a snow cover over a considerable area of habitats, since falling snow is blown away to lower belts often before it even reaches the ground. Although in many cases this belt, occupying a higher position along the profile, has the highest winter precipitation, it has the thinnest snow cover over most of its area. Another feature is the very abrupt changes in temperature and moisture, including those occurring over several days, which characterize the climate of this belt as more continental in comparison with the lower belts. These factors determine the preponderance of physical erosion over chemical and biological erosion, and the predominance of rocky streams and scree.

A dramatically shortened season of growth (30-70 days) is characteristic for the belt of cold bald-peak deserts. Nevertheless, photosynthesis in lichen growing on rocky blocks occurs at temperatures close to 0°C. Likewise important is the fact that the territory of this belt is enshrouded in clouds sometimes continuously for a period of many days.

First of all, we shall discuss the floristic features of the belt of cold bald-peak deserts. We place the plant species found here in three categories: 1) chracteristic only of this belt; 2) having their maximum altitudinal circumscription in this belt, but occurring in lower belts; 3) encroaching from lower belts where their maximum altitudinal circumscription occurs. Only species in categories 1 and 2 will be described below for the belt of cold bald-peak deserts. The affiliation of species with certain floristic elements is indicated by abbreviations: A, arctic; Al, alpine; AAl, arctoalpine; AlA, alpine-arctic (distributed predominantly in the Arctic, but rare or found only in northern mountains in more southern high mountains); HAM, hypoarctomontane; HAA, hypoarctoarctic.

<u>The Kola Peninsula — Khibiny Mountains</u>. The belt of bald-peak deserts (Serebryakov and Kuvaev, 1951;* Mishkin, 1953) occurs above (850) 900-1100 m. Most characteristic are

* Omitted from "Literature Cited" section in the Russian original — Publisher.

Huperzia selago ssp. arctica (A), Deschampsia alpina (A), Poa arctica (AlA), Luzula arcuata (HAA), L. confusa (AAl), Salix herbacea (AAl), S. polaris (AAl), Silene acaulis (AAl), Oxygraphis vulgaris (AAl), Ranunculus pygmaeus (AlA), R. sulphureus (A), Cardamine bellidifolia (AAl), Saxifraga oppositifolia (AAl), S. rivularis (A), and Cassiope hypnoides (A).

Of the listed species, six belong to the arctic element of flora. Luzula arcuata is a transitional species between strictly arctic and hypoarctic plants. The other species are unquestionably arctoalpine. Plants typical for the European Arctic are Luzula arcuata, Oxygraphis vulgaris, and Salix herbacea (the last species is also found in the eastern American Arctic).

Circumpolar Urals. This is the section of the Ural mountainous region with a highly developed landscape of cold bald-peak deserts (Gorchakovskii, 1975; Kuvaev, 1969). The section from the Bolban-yu River to the sources of the Khulga River can be easily compared with other mountain systems. The boundary between the mountain-tundra belt and the belt of cold bald-peak deserts meanders, but generally occurs at 810 m. Vascular plants noted here include Huperzia selago ssp. arctica (A), Luzula confusa (AAl), L. nivalis (A), Salix nummularia (AAl), S. polaris (AAl), S. reptans (A), Oxygraphis glacialis (AAl), Ranunculus pygmaeus (AlA), Cardamine bellidifolia (AAl), Parrya nudicaulis (AlA), Saxifraga rivularis (A), Sieversia glacialis (AlA), Potentilla emarginata (A), Cassiope hypnoides (A), C. tetragona (A, it is sometimes found in high mountains of the boreal zone), Pedicularis lanata var. dasyantha (P. dasyantha, A), Nardosmia gmelinii (AAl), Senecio atripurpureus (A), and Crepis chrysantha (AlA). In this list, nine are strictly arctic species, four are alpine-arctic, and five are arctoalpine. The proportion of arctic species increases as one proceeds from the area with an oceanic climate (Kola Peninsula) to the more continental region of the Urals.

Putorana. The higher altitudes of high mountains in Putorana have not been extensively studied. Here the belt of cold bald-peak deserts occurs above (1100) 1200-1300 m (Kuvaev, 1976; Vodip'yanova and Krogulevich, 1974; "Flora of Putorana," 1976). Associated most frequently with this region are Deschampsia brevifolia (A), Poa arctica (AlA), Poa paucispicula (A), Festuca brachyphylla (AAl), Carex macrogyna (AAl), Luzula confusa (AAl), L. tundricola (A), Papaver radicatum (A), Cardamine bellidifolia (AAl), Parrya nudicaulis (AlA), Saxifraga caespitosa (AlA), S. rivularis (A), Potentilla uniflora (A), Sieversia glacialis (AlA), Pedicularis hirsuta (A), Senecio resedifolius (AAl), Saussurea tilesii (A), Taraxacum arcticum (A), Stellaria fischeriana (AlA), and Ranunculus sulphureus (A). Of the 20 species listed, half are arctic, one fourth are alpine-arctic, and one fourth arctoalpine.

Verkhoyanski Mountains. Found in the belt of cold bald-peak deserts in the Verkhoyanski Mountains (Kuvaev, 1979; Yurtsev, 1968) are 16 species, of which two are also typical for plexus of Suntar-Khayata mountains (Yurtsev, 1968): Huperzia selago ssp. arctica (A), Festuca auriculata (AAl), Carex misandra (AlA), C. rupestris (AAl), Juncus biglumis (AlA), Luzula confusa (AAl), Lloydia serotina (AAl), Ranunculus sulphureus (A), Cardamine bellidifolia (AAl), Potentilla elegans (AAl), P. uniflora (A), Sieversia glacialis (AlA), Lagotis minor (A), Pedicularis oederi (AAl), and Taraxacum arcticum (A), Senecio resedifolius (AAl) is arbitrarily included in this group of species; it is equally typical both for the belt of cold bald-peak deserts and for the belt of mountain tundras. Some species emerging as mountain-tundra species in the western sector of the Subarctic (Festuca auriculata, Carex misandra, C. rupestris, Lloydia serotina, Lagotis minor, Pedicularis oederi, and Senecio resedifolius), are more closely associated here with the belt of cold bald-peak deserts. The role of the arctoalpine element increases on this account: There are eight strictly arctoalpine species here, and three alpine-arctic; the arctic element becomes subordinate (five species). Found among these are plants from eastern Siberia and the Siberian (predominantly) Subarctic and Arctic (Festuca auriculata, Potentilla elegans, and P. uniflora).

Mountains of the Far East. The belt of cold bald-peak deserts is extensive in the Far East, and this landscape extends far to the south (Shlotgauer, 1978;* Katenin, 1976; Polezhaev et al., 1976; Kharkevich and Buch, 1976; Balandin, 1978). Despite the difference in the flora of continental and maritime high mountains of the Far East, we still find it necessary to treat them as a single unit, and therefore the proposed list is not uniform. It

* Omitted from "Literature Cited" section of Russian original — Publisher.

includes 21 species: Dryopteris fragrans (AA1), Selaginella sibirica (HAM), Huperzia selago ssp. arctica (A), Calamagrostis arctica (A1), Poa kolymensis (A), Festuca brachyphylla (A1), Carex rupestris (AA1) Luzula confusa (AA1), Salix berberifolia ssp. kamtschatica (A1), S. phlebophylla (AA1), Silene stenophylla (AA1), Draba stenopetala (A), Saxifraga bronchialis ssp. funstonni (AA1), Potentilla elegans (AA1), P. uniflora (A), Oxytropis tschuktschorum (A1A), Cassiope ericoides (AA1), Eritrichium ochotense (A1), Pedicularis adamsii (A), P. lanata (A1A), and Artemisia furcata (AA1). The role of the arctic element here is smaller; there are only five strictly arctic species. Species from the more southern arctoalpine element and alpine species (more specifically, bald-peak species in this case) have the advantage here. There are three species intermediate between the last two elements. By range type, the flora is characterized by an abundance of American-Asiatic species (Dryopteris fragrans, Selaginella sibirica, Calamagrostis arctica, Salix phlebophylla, Fraba stenopetala, Potentilla uniflora, Oxytropis tschuktschorum, Artemisia furcata) and the high participation of Far-Eastern endemics (Poa kolymensis, Salix berberifolia ssp. kamtschatica, Eritrichium ochotense).

As is evident, the species composition of flora in the belt of cold bald-peak deserts is not constant at the same longitudes. Six species and subspecies are typical in this belt for almost all sectors of the Subarctic: Huperzia selago ssp. arctica, Luzula confusa, Ranunculus sulphureus, Cardamine bellidifolia, Saxifraga rivularis s.l., and Sieversia glacialis. The differences in species composition are partially determined by the presence of plants endemic to or associated with certain longitudes. If species gravitating toward the Atlantic basin and the western Arctic basin are typical for cold bald-peak deserts in the Khibiny Mountains (Salix herbacea, Oxygraphis vulgaris, etc.), then species typical near the Pacific Ocean and generally more eastern species appear in the Verkhoyanski Mountains (Potentilla elegans, P. uniflora, Festuca auriculata, etc.). Moreover, transition of species from one altitudinal cenotic group to another is observed because of changes in conditions of different longitudes. Thus, Cassiope tetragona is a bald-peak desert species in the northern circumpolar Urals, but becomes a typical mountain-tundra species east and west of the Urals to the Khibiny, Putorana, and western Verkhoyanski Mountains; Juncus biglumis, Lloydia serotina, Pedicularis oederi, etc., are typical mountain-tundra species in the west; toward the east they move upwards along the profile and become inhabitants of the cold bald-peak deserts.

Thus, the floristic features of the belt of cold bald-peak deserts, if regarded from the viewpoint of vascular plants, are determined: 1) by the presence of a few species found almost exclusively in this belt practically throughout the entire Eurasian Subarctic; 2) by the presence of a series of species typical for this belt in some sector of the Subarctic; and 3) by the universal presence of groups of species associated primarily with this belt or having the greatest distribution and maximum high circumscription in it (the group includes species capable of occupying lower positions along the profile in other mountain systems of the Subarctic).

Cryptogamous plants, lichen and mosses, play a much greater role in the formation of the plant cover in the belt of cold bald-peak deserts. Of lichen, epilithic species (Rhizocarpon geographicum, etc.) predominated, but endolithic species with thallomes penetrating into stone are especially typical (some species of Aspicilia, Verrucaria, and others). Also numerous are foliose epilithic lichen, primarily from the family Umbilicariaceae. Many species encountered here attach to stones with a small section of the thallus by means of a gomphus.* Of the foliose lichen attaching by rhizoids, common are the small-leaved lichen, generally growing closely together on the rock surface (Parmelia centrifuga, P. stygia, and others). Typical for fruticose lichen are species forming dense hemispheric tufts (Sphaerophorus fragilis, Stereocaulon vesuvianum, and others).

Especially abundant among mosses are species forming hemispheric solid cushions on the surfaces of crags and rocks: Andreaea rupestris s.l. and Grimmia spp. Cushions of Chandonanthus setiformis generally fill the deep cracks among clumps, and likewise luxurious slab-like cushions of Rhacomitrium lanuginosum on rubbly areas with trickling water. The predominance of cushion-forming epilithic bryophytes is typical in general for the belt of cold bald-peak deserts.

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* A Russian botanical term for a peg-like or stalk structure — Translator.

In contrast to the belt of mountain tundras where the plant cover is solid or almost solid, vegetation is fragmentary in the belt of cold bald-peak deserts. Competition among plants is expressed only to a limited extent. The conflict among plants appears predominantly under unfavorable environmental conditions. There are no phytocenoses with a well-developed composition and structure or developed aboveground and underground layers. Labile plant groups in the early stages of syngenesis predominate.

CONCLUSIONS

The boundaries of belts in mountains are the critical altitudinal levels where a more or less abrupt qualitative change in ecosystems (biogeocenoses) and in their major component, vegetation, occurs under the influence of environmental parameters (primarily climatic factors), which change gradually with altitude. These boundaries are subject to fluctuations primarily on a background of variable climatic conditions.

Thus, for example, in the Khibiny Mountains the timberline in the Holocene ascended repeatedly and then descended, as indicated by finds of tree trunks and podzolic soil in mountain tundras and also by the presence of solifluction terraces and rocky detritus in the forest belt. The last major ascent in forests in mountains ended 800-900 years ago, when forests reached a level of 520-550 m (its current limit is 400 m); then conditions deteriorated, the boundary dropped to 270-300 m, and about 200 years ago began to ascend again as the climate improved (Ryabtseva, 1970). Relict highland terraces, now found in the mountain-forest belt but formed earlier under the influence of solifluction and frost erosion in the belt of mountain tundras in a more severe climate when the timberline was lower, are also encountered in the Urals.

Fluctuations in the timberline and, consequently, in the boundary between the "subpeak" and mountain-tundra belts are readily traced in the Urals on the basis of dendrochronological data (Gorchakovskii and Shiyatov, 1985).

The nature of altitudinal belts of vegetation in a certain mountainous region depends primarily on its zonal position, altitude, and mountain mass. The systems of altitudinal belts cannot be universal; they should be defined to suit large territorial subdivisions of the plant cover not on the basis of formal criteria (geomorphological, floristic, etc.) but on an ecological basis with consideration of the entire aggregate of characteristics. The absoluteness of the "alpine template" of belts, as well as the use of vague terminology for belts (lower, middle, upper), does not reflect current theories on patterns of plant cover distribution or the requirements of theoretical and applied sciences. Preference should be given to systems of belts, developed for large plant geographic regions on the basis of composition, structure, and seasonal rhythms of vegetation. Belts should be named on the basis of features of the predominant ecosystems (biogeocenoses) and their major components, the plant communities.

The following belts of vegetation should be defined in conformity with the concept on a close relationship between vegetation belts and the zonal position of a certain mountain system in mountains of the boreal zone of the USSR: "subpeak," mountain-tundra, and the belt of cold bald-peak deserts.

"Subpeak" Belt. It is characterized by more or less open low-growing forests, i.e., low forests and elfin woodlands in combination with mesophilic meadows.

"Mountain-Tundra Belt. This occurs above the previous belt. Mountain tundras (stony, lichen, dwarf shrub-moss, shrub-moss, and grass-moss) predominate here in combination with areas of snowline cryophilic meadows.

Belt of Cold Bald-Peak Deserts. These are found on the highest mountain peaks with the most severe climate. The growth season is very short; vegetation is dispersed with communities of epilithic lichen and some mosses predominating. Flowering plants and ferns are encountered only as single specimens in rock crevices. In this belt, there are typical species of lichen, mosses, and some species of flowering plants primarily associated with it.

The determination of differences in vertical differentiation of the plant cover in mountainous regions differing in zonal position is one of the major recent achievements of geobotany, plant ecology, and biogeography, and has facilitated the more thorough study of high mountains on a comparative basis.

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