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ECOLOGY OF BOREAL RELICS IN FOREST OASES OF CENTRAL KAZAKHSTAN

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Boreal relics are used to trace features of the existence of small populations of plants at the limit of their geographic and ecological range: Segregation, a shift in ecological optimum, transition to uncharacteristic phytocenoses, and the "edge effect."

In the Central Kazakhstan Physicogeographic Nation (Gvozdetskii and Nikolaev, 1971) there rise small vocanos, uplands, and insular hills above the surface of denudational and accumulative plains (mountains of from 1000 to 1500 m above sea level in elevation; granite intrusions with steep slopes, rocky crests, and granite outcrops). Preferentially associated with such strongly eroded granite hills are tracts and portions of pine forests and sparse forests, as well as individual occurrences of pine.

A large portion of the granite hills is concentrated within the Kokchetavsk Upland. Sinyukha Mountain (887 m above sea level), the Kokshetau Range, and the mountains Imantau (661 m above sea level) Zerendinsk (586 m above sea level), Airtau, Sandyktavsk, and others are found here.

At a considerable distance from the Kokchetavsk Upland, to the south, are the Bayanaul'sk (1027 m above sea level) and the Karkaralinsk (1403 m above sea level) hills. Furthermore, the small granite masses Kent (1469 m above sea level), Kuu, Kyzylrai (1555 m above sea level), and Bakhty are located in the region of the Karkaralinsk Mountains.

By their position and several other features the insular forest tracts of Central Kazak Kazakhstan can be divided into two groups — the Kokchetavsk and the Baynaul'sko-Karkaralinsk (see Fig. 1). All these tracts are in the steppe zone; moreover, the Kokchetavsk group is in the subzone of forb–feather grass steppe, while the Bayanaul'sko-Karkaralinsk, in the subzone of dry sheep's fescue–feather grass steppe (Map of Vegetation of Steppe Portion of Kazak Hill Country, 1975). However, the granite intrusions rising above the surrounding territory disturb the pattern of the zonal distribution of vegetation; therefore, their lower levels belong to the forest-steppe, and higher levels, to the forest belt, forming unique forest oases among the surrounding steppes.

The Kokchetavsk group includings the Borovsk, Makinsk, Imantavsk, Airtavsk, Zerendinsk, and Sandyktavsk forest tracts. Pine grows here on granite hills (Kokshetau Range, Sinyukha, Imantau, and Airtau mountains) or on lower uplands made up of metamorphic rocks. The most boreal aspect is that of the Borovsk Tract, within which open sphagnum bogs, as well as ryams (sphagnum bogs overgrown by low pine) and sogras (boggy birch stands with semi-flowing moisture, sometimes with an admixture of pine) have been preserved on the edges of the lakes Karas'ee, Svetloe, and Shchuch'ee. The presence of sphagnum peat bogs and boggy forests in the hills of the Kazakh Hill Country, at a substantial distance from the southern limit of their major distribution and in the vicinity of steppe, represents a unique botanico-geographic paradox.

The Bayanaul'sko-Karkaralinsk group of forest oases includes the Bayanaul'sk and Karkaralinsk tracts, as well as the small islands of pine forest on the mountains Kent, Bakhty, Kuu, and Kyzylrai.

In the Kokchetavsk group of forest oases the pine stands associated with granite intrusions are distinguished by a high closure and are stable with respect to anthropogenic impacts. The forests in this group of oases have a more boreal aspect; associations are encountered here with a pronounced cover of green nitid mosses (rocky–mossy and mossy–herbaceous associa-

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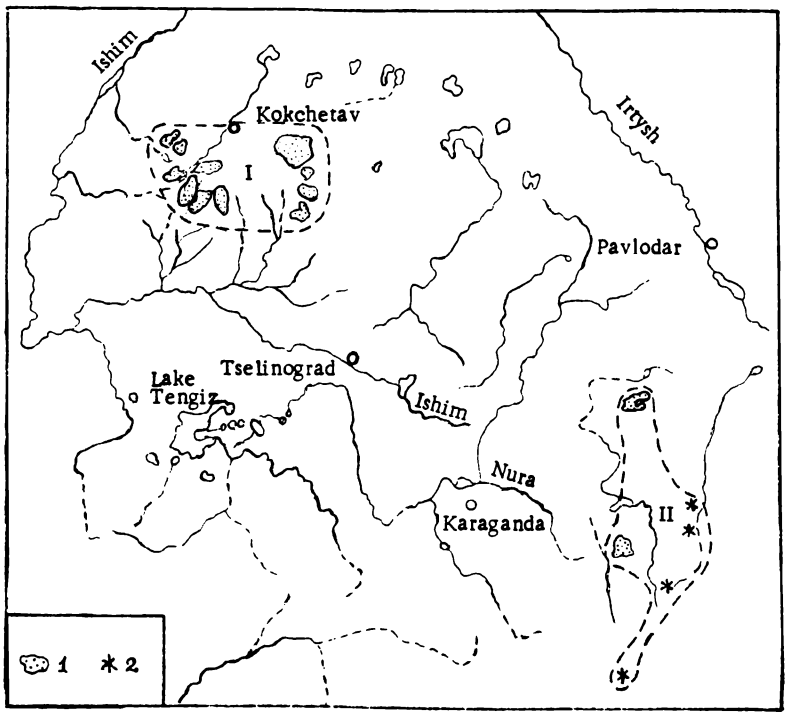

Fig. 1. Schematic map of forest oases: I) Kokchetavsk group, II) Bayanaul'sko-Karkaralinsk group; 1) pine forests, 2) small portions of pine forest at limit of range.

tions), while those in the closed or semiclosed basins have sphagnum bogs and bogy forests. Forb and forb–grass pine forests are widespread on the metamorphic mountain rocks.

In the Bayanaul'sko-Karkaralinsk groups of forest cases, where the climate is more arid, the conditions are less favorable for pine growth. The distribution of pine in this region is limited to the granite intrusions; pine is not encountered outside their limits on other mountain rocks. The forests here are in general sparser, widely distributed, unique, arid–petrophytic sparse forests (Gorchakovskii and Lalayan, 1982). The rockiness of the substrate, and the weakening or complete loss of the edificator role of the tree stratum in sparse forests determine the predominance in the herbacous cover of petrophytes and steppe and forest-steppe species; boreal relics are absent or encountered sporadically.

The isolated pine tracts of the hills are more or less steppified; however, they are the nucleus for a complex of plants characteristic of the boreal (coniferous-forest) zone. The encounter of boreal plants far from their major distribution range, in the vicinity of dry steppes, is of great interest for botanical geography and ecology. There is no doubt in the relic nature of this complex of species, formed in the past under conditions of a cooler and moister climate, when there existed (and were later interrupted) migratory bridges linking the forest vegetation of Central Kazakhstan with the zonal taiga of Western Siberia and the mountain forests of the Urals and Altai.

Data on boreal relics in the mountain-steppe tracts of Kazakhstan were reported in the work of Gordyagin (1900-1901), Semenova (1926, 1928, 1930), Denisova (1962, 1971, 1973), and others. As a result of our investigations the list of boreal relics has been greatly complemented, their habitats and growing conditions have been characterized, and also certain factors and mechanisms enabling the existence of small isolated populations of boreal plants under conditions of an arid climate with a pronounced secular and intrasecular cyclicity of hydrothermic conditions have been revealed.

Study of boreal relics in the flora of Kazakhstan will permit clarification of the history of the formation of the plant cover of this territory, to estimate better its current conditions, and also to foresee its future changes against the background of changing environmental conditions and intensifying anthropogenic impacts. Populations of boreal relics are of indicational value, and they can be used with success for environmental monitoring and estimation of the level of anthropogenic degradation of the plant cover. Furthermore, it should be borne

in mind that certain representatives of this complex are decorative, food, medicinal, and technical plants. They all enrich the local flora, enhance its agricultural value, and occupy a definite place in the natural economy; the stability and the very existence of several ecosystems depends upon their presence.

BOREAL RELIC FLORA OF FOREST OASES

A complex of boreal mosses is associated with the insular pine forests. Although the moss cover in insular pine forests is in general more poorly developed than in the northern taiga, nevertheless in some habitats (north slopes of granite slopes and crests, stream banks, bogs, sogras), mosses play an important role in the makeup of plant communities. We found a total of 60 moss species in the forest tracts of the Kazakh Hill Country belonging to 36 genera and 23 families. Nearly the entire set of moss species characteristic of the northern taiga (including Hylocomium splendens, Pleurozium schreberi, Rhytidiadelphus triquetrus, Ptilium crista-castrensis) and peat bogs (eight species of the genus Sphagnum, Aulacomnium palustre) is represented here. Only the absence of Polytrichem commune is noted. The growth in insular pine tracts of many taiga and bog mosses emphasizes the primary boreal nature of these plant communities and serves as additional evidence for their former connection with the northern taiga.

Boreal-relic (in the broad sense of this concept) vascular plants are represented by 110 species. They belong to 73 genera and 36 families. They include 63 forest and meadow-forest, 39 bog, 5 rock-associated species, and one species with a broad ecophytocenotic amplitude.

The forest plants are represented by the ferns Gymnocarpium dryopteris, Athyrium filix-femina, Dryopteris carthusiana, clubmosses Lycopodium clavatum, Diphazium complanatum, the twin flower Linnaea borealis, recumbant goodyera Goodyera repens, the pyrolas Pyrola rotundifolia, P. minor, P. chlorantha, Moneses uniflora, Chimaphila umbellata, triental Trientalis europaea, coral root Corallorhiza trifida, cowberry Vaccinium vitis-idaea, whortleberry V. myrtillus, and others.

Among the bog plants there should first be mentioned Oxycoccus palustris, Drosera rotundifolia, D. anglica, Eriophorum angustifolium, E. gracile, Rhynchospora alba, Spiranthes amoena, and many sedge species.

The presence of typically taiga and bog plants in the forest oases of Central Kazakhstan approximates their flora to the flora of the northern taiga. However, it cannot be overlooked that no series of plants characteristic of northern peat bogs (Ledum palustre, Chamaedaphne calyculata, Andromeda polyfolia) nor the typically taiga species, the May lilly (Majanthenum bifolium), is present here.

Belonging to the group of rock-associated plants are the ferns Woodsia ilvensis, Cystopteris fragilis, Polypodium vulgare, Siberian saxifrage Saxifraga sibirica, and the currant Ribes saxatile.

Standing apart is Dasiphora fruiticosa, a component of the Pleistocene floristic complex characteristic of open, sparse forests, shrub stands, tundras, bogs, and exposed rocky, gravelly, and sandy substrates (Gorchakovskii, 1969). In the Urals and in the Kazakh Hill Country this is a relic of the epoch of maximum glaciation. The penetration of D. fruticosa into the Borovsk forest tract during the Pleistocene coincided with the invasion here of many taiga and bog plants, preserved here up to the present time in the position of relics.

Dryopteris filix-mas and Aegopodium podagraria can be provisionally classed as boreal relics. They essentially belong to the boreal-nemoral complex: In the center of their range they are mainly associated with broad-leaved forests, but on the periphery of the range they are also found in plant communities of other types.

CHARACTERISTIC HABITATS OF BOREAL RELICS

Boreal relics are associated with the following, most characteristic ecotopes: The sites of discharge of springs, the shores of streams, the valleys of intermittent streams, lake shores, quaking bogs on the shore region of lakes, sphagnum bogs, ryams and sogras, fissures in granite blocks, the rocky crests of mountains, the niches at their feet, mossy and mossy–herbaceous pine forests on the slopes and shelves of the highest mountains, and European alder forests.

Sites of Spring Discharge. Near springs with their continuous flowing moisture are concentrated the habitats of the rare orchids Ciprypedium calceolus, C. macranthum, Dactylorhiza

fuchsii, D. majalis, and D. maculata. Corallorhiza trifida grows in the moss bed along the banks of the streams draining the springs. Also found here are the pyrola species Pyrola rotundifolia and P. minor and the fern Gymnocarpium dryopteris, and others.

Stream Banks. Along the banks of streams, especially in deep shady canyons are found thickets of small trees Padus racemosa, Salix caprea, Crataegus altaica, Sorbus sibirica and the shrubs Ribes nigram, R. hispidulum, and Viburnum opulus. The ferns Athyrium filix-femina, and Pteridium aquilinum are abundant here; Heracleum sibiricum, Angelica sylvestris, Scirpus sylvaticus, Rubus idaeus, and Galium boreale are numerous; Lysimachia vulgaris, Naumburgia thrysiflora, Pleurospermum uralense, Filipendula ulmaria, Geranium sylvaticum, Ligularia sibirica, Crepis sibirica, Equisetum sylvaticum, E. pratense, Pyrola rotundifolia, and P. minor are common; Dactylorhisa maculata is rare.

Valleys of Intermittent Streams. The hill slopes are in places drained by streams that run after rains but disappear during the dry times of year. Such intermittent streams are characteristic, for example, of the slope of Mount Imantau, which faces the lake of the same name. The boreal flora of the valleys of intermittent streams is more impoverished: Ribes nigrum, Salix caprea, Salidago virgaurea, Rubus saxatilis, Galium boreale, and some others.

Lake Shores. Lakes exert a moistening and moderating influence on the meso and microclimate of the surround locality. Here in the summer fogs frequently gather, dew falls, and the fluctuations in temperature are not so severe. The habitats of many boreal relics are associated with the fringes of lakes. Thus, the hill-country clubmosses Lycopodium calvatum and Diphazium complanatum, extremely rare in the Kazakh Hill Country, are found on the shore of Lake Karas'eo. The ferm Pteridium aquilinum is quite common along the fringe of lakes Karas'ee and Svetloe; the rare species Dryopteris carthusiana grows here. The exceptionally rare species Trientalis europaea has been preserved on the shores of lakes Svetloe and Zerkal' noe. It grows in groups of individuals in pine–birch forest on peat soil, on the mounds at the base of birch trunks. Equisetum hyemale forms whole thickets in the vicinity of lake Borovoe at the mouth of Imanaisk Spring. A nearly continuous thicket of Equisetum sylvaticum growing on strongly peated soil enriched with mineral layers delivered by rain waters from the slope extends on the north shore of L. B. Karas'ee, in a long band in contact with a narrow quaking bog (1-1.5 m). Cowberry Vaccinium vitis-idaea is also found primarily near lakes. It is numerous on the anient terraces of L. Svetloe, where it grows in pine forests on deep gravelly soil.

Quaking Bog on Lake Shore. The quaking bog on the shores of lakes Karas'ee, Borovoe, and Svetloe serve as a characteristic habitat of fern Thelypteris palustris, in places forming solid thickets. Equisetum palustre and E. fluviatile are also found here.

Sphagnum Bogs, Ryams, and Sogras. Associated with these communities is a complex of species characteristic of the bogs of northern taiga: Salix lapponum, Oxycoccus palustris, Drosera rotundifolia, D. anglica, Rhynchospora alba, Eriophorum angustifolium, E. gradile, pedicularis palustris, P. sceptrum-carolinum, Spiranthes amoena, Carex vaginata, C. rostrata, C. rostrata, C. buxbaumii, C. irrigua, C. hartmanni, Menyanthes trifoliata, and others. Also on hummocks here are the refuges of several plant species that under zonal conditions usually grow in coniferous taiga: Linnaea borealis, Goodyera repens, Vaccinium vitis-idaea, Pyrola rotunifolia, P. minor, and others.

Fissures in Granite Blocks. The rocky remnants on the crests and slopes of mountain and ranges provide a refuge to Rubus idaeus, as well as the ferns Asplenium septentrionale, Polypodium vulgare, Woodsia ilvensis, and Cystopteris fragilis colonizing the fissues filled with wood and fine earth. On the rocky crest of Sinyukha (south slope) grow Dasiphora fruticosa, and Chamaenerion angustifolium, while Saxifraga sibirica grows in shady damp fissures on the north slope.

Niches at Foot of Rocky Mountain Crests. On the north slopes of the higher mountains and crests at the base of broken rocky crests during the winter considerable snow accumulates, the melting of which is delayed until early or mid June. In shaddy places protected from the wind, among the large rocky remnants a rather thick layer of fine earth forms; moisture is abundant due to the snow melt, the rain water draining from the rocky crests, as well as the condensation of water vapor in fissues. Such shaddy niches serve as habitat for a series of relic plants. Thus, Juniperus communis grows in niches at the foot of crest of Mt. Sinyukha in the form of shrubs and small trees (up to 3 m); in more open sites it assumes a dwarf form. Rubus idaeus, Ribes nigrum, the ferns Athyrium fillix-femina, and the boreal-nemoral relic fern Dryopteris filix-mas are found here.

Mossy and Mossy–Herbaceous Pine Forests on Slopes and Shelves of Highest Mountains. The steep northern slopes of large mountains (such as, for example, the north slope of Mt. Sinyukha, facing M. Cherbach'ee Lake) are typically rocky; the granite blocks are covered by green mosses and lichens. Pine trees grow between the blocks. The shelves of are less rocky, are enriched by fine earth, and the herbaceous cover is better developed. Linnaea borealis, Goodyera repens, Necttianthe cucullata, Moneses uniflora, Chimaphila umbellata, Ramischia secunda, Pyrola chlorantha, P. rotundifolia, and P. minor, the ferns Gymnocarpium dryopteris, G. robertianum, and G. tenuipes, and others grow in the mossy and mossy–herbaceous pine forests.

European Alder Forests. The communities of European alder(Alnus glutinosa), found in stream valleys and often in deep shady canyons (Gorchakovskii and Lalayan, 1981), serve as refuges for many boreal relics. The growth of boreal species in alder forests is favored by the abundant flowing moisture, the rich soil, the well-developed forest litter, and shading by the tree canopy. Circaea alpina, C. luteciana, Delphinium elatum, Athyrium filix-femina, Matteuccia struthiopteris, Pyrola rotundifolia, and others are found here.

The common factor that unites all these ecotopes is protection from fires, the presence of a reserve of moisture during dry periods, and provision with a constant static, semi-flowing, or flowing moisture due to the discharge of springs, proximity of ground waters, the condensation of water vapor present in the air, and the moistening influence of lakes.

PATTERNS OF DISTRIBUTION AND SITES OF CONCENTRATION OF BOREAL RELICS

The sites of the greatest concentration of boreal relics are provided by the Borovsk, Imantavsk, Sandyktavsk, Bayanaul'sk, and Karkaralinsk mountain-forest tracts. Certain boreal relics (Pyrola rotundifolia, P. chlorantha, Ramischia secunda, Moneses uniflora, Chimaphila umbellata, and Necttianthe cucullata) are widespread both in the Kokchetavsk and in the Bayanul'sko-Karkaralinsk group of insular forests. However, a substantial portion of the relics have a more limited distribution.

The Kokchetavsk group of forest tracts is highly saturated with relics; Goodyera repens, Linnaea borealis, Pyrola minor, Vaccinium vitis-idaea, Lycopodium clavatum, Diphazium complanatum, and others are found only here. Among the insular forests of the Kokchetavsk group the Borovsk forest tract is distinguished by an especially high content of relics. This is promoted by the sharply dissected relief with relatively high ranges (Kokshetau, Sinyukha), the abundance of interconnected lakes, the presence of sphagnum bogs, ryams, and sogras. Most relics of the bog complex grow only in the Borovsk tract: Drosera rotundifolia, D. anglica, Eriophorum gracile, Rhynchospora alba, Spiranthes amoena, Pedicularis sceptrum-carolinum, P. palustris, Epipactis palustris, Carex viginata, C. limosa, C. omskiana, C. irrigua, Liparis loeseli, Menyanthes trifoliata, Viola epipsila, and Salix lapponum. Dactylorhiza maculata, D. majalis, Cypripedium caleolus, C. macranthun, Jinperus sibirica, and Huperzia selago and Dryopteris carthusiana, first found by us, are encountered only here. Vaccinium myrtillus is found only in the Sandyktavsk forest tract.

The set of relics associated exclusively with the Bayanaul'sko-Karkaralinsk group of insular forest tracts is small. These include Deophinium elatum, Impatiens noli-tangere, and Circaea alpina. The distribution of Malaxis monophyllos and Circaea luteciana is limited to the Bayanaul'sk tract; that of Aconitum excelsum, Bupleurum aureum, and Carex loliacea, to the Karkaralinsk tract; and C. capillaris, to the Kentsk.

FEATURES OF REFUGES AND ECOLOGY OF BOREAL RELICS

The refuges of boreal plants are associated with habitats where the moisture conditions (surface and ground) have always remained favorable without undergoing catastrophic changes. These refuges are hills with a pronounced vertical stratification of the vegetation, with a dissected relief, rocky mountain summits, deep valleys, canyons, closed basins, freshwater lakes, springs, rivers, and lakes.

During the Holocene the overall environmental conditions have not remained constant; in particular, cyclic changes in moisture conditions have occurred. Boreal relics could survive only where there was a permanent, additional source of moisture even during dry periods of the year (due to the emergence of fissure waters, the proximity of ground waters, the condensation of atmospheric moisture, the collection of atmospheric precipitation from slopes). Another necessary condition for the survival of relics was a sufficient ecological diversity of neighboring plant communities, with the consequent provision for the possibility of the

migration of populations of relic species from one community to another (for example, their passage from forest to bog during increasing aridity, the return to the forest upon an increase in moisture). Specifically the boundary strips of neighboring plant communities differing in moisture conditions have always been the most favorable refuges for boreal relics ("edge effect").

In the major part of their range, within the forest zone on plains, boreal plant species grow under various environmental conditions and have a rather broad ecological amplitude. However, in the insular forests of the Kazakh Hill Country they have been able to survive only under their optimal environmental conditions. The ecological optima of many species in the north and in Kazakhstan do not coincide; the ecological optimum of boreal relics in steppe forests is shifted towards greater edaphic moisture, which compensates for the insufficiency of atmospheric moisture (low humidity). The shift in the ecological optimum of boreal relics (with respect to the moisture gradient) is accompanied by their transition to other habitats and plant communities that are usually uncharacteristic of them.

Thus, many typical taiga plants such as Goodyera repens, Linnaea borealis, Corallorhiza trifida, Moneses uniflora, Ramischia secunda, Chimaphila umbellata, Pyrola rotundifolia, P. minor, Equisetum sylvaticum, Trientalis europaea, and others pass from drained habitats to overmoistened habitats in sphagnum bogs, and in ryams and sogras, where they grow on hummocks or on the fringes of the bog tracts. The distribution of these species in forests is limited by the low humidity and the instability of the soil moisture; in bogs the near-ground layer of air is moister, while the soil moisture is stable.

Boreal plants penetrated the region of the Kazakh Hill Country primarily during the Pleistocene, when the climate was moister and cooler. The connecting links between the mountain forests of Kazakhstan and the forest of the Southern Urals, Western Siberia, and the Altai might have been provided by the forests of the Turgai Basin (such as the Aman-Karagai) in the west, the valley of the Ishim River in the north, and the narrow forests of the Irtysh region to the east.

At the present time boreal relics are concentrated in a few habitats with special environmental conditions most favorable for them and resulting from a rare, and sometimes unique combination of topographic, edaphic, hydrologic, and microclimatic factors. Here they could be preserved, surviving drought epochs, when the forestation and water supply of the territory declined.

CONCLUSION

At the limit of the geographic and ecological range, in Central Kazakhstan, where the major limiting factor is the lack of atmospheric moisture, the complex of boreal plants, found here in the position of relics, is greatly impoverished, and the life strategy, ecology, and cenology of its component species are characterized by the following features:

segregation – the separation from the boreal complex of small groups ("migrations") of species united by a similar ecology, and their independent existence in various ecological niches, in a few ecotopes with an especially favorable combination of external factors;

partial compensation for the lack of atmospheric moisture by more abundant and sufficiently stable soil moisture;

shift in ecological optimum of individual species along ecotopic profile towards moister ecotopes;

transition of the "migrations" of species or individual relic species from phytocenoses characteristic of them in the center of their abundance (in boreal zone) to phytocenoses usually uncharacteristic of them (for example, forest species in sphagnum bogs);

preferential association of location of certain relic plants with boundary zone between phytocenoses differing in moisture regimen ("edge effect"), which promotes the survival of populations by enabling the migration of plants from one community to another in the course of cyclic climate changes.

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