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## Chapter 2

# ECOLOGICAL RANGES OF PLANT SPECIES IN THE MONSOON ZONE OF THE RUSSIAN FAR EAST

*Vitaly P. Seledets<sup>1\*</sup> and Nina S. Probatova<sup>2</sup>*

<sup>1</sup>Pacific Institute of Geography FEB RAS, 690041 Vladivostok, Russia

<sup>2</sup>Institute of Biology and Soil Science FEB RAS, 690022 Vladivostok, Russia

## ABSTRACT

The monsoon zone covers a considerable part of the Russian Far East (RFE), which includes the Kamchatka Peninsula, Sakhalin, the Kurile Islands, the continental coasts and islands of the Bering Sea, the Sea of Okhotsk, the Sea of Japan, and the Amur River basin. The problem of biodiversity in the monsoon zone is connected to species adaptations, speciation and florogenesis, the formation of plant communities, vegetation dynamics, and population structure. Our concept of the ecological range (ecorange, ER) of plant species (Seledets & Probatova 2007b) is aimed at adaptive strategies in the RFE monsoon zone compared with Inner Asia. Every species has its own ER, which changes in different parts of the species geographical range. The ER is part of a multidimensional ecological space (MES). Grades of ecological factors were estimated by the scales of L.G. Ramensky, which we modified for the monsoon zone of the RFE. The ER of plant species is a complex of coenotic populations (coenopopulations) within the geographic range of the species. We distinguish a holoeorange (HER, part of ecological space, where the species is able to exist) and a coenoorange (CER, where the species predominates in plant communities). The ER is characterized by dimensions, configuration, and orientation in the MES, by effectiveness (CER/HER ratio) and also by the ecological optimum and the center of the HER, which coincide in some cases (symmetrical ER) but not in others (asymmetrical ER). The position of the ER in the MES indicates the area of the species' ecological adaptation. The configuration of the ER shows the path of ecological adaptation. HERs show the ability of taxa to occupy a certain part of the MES. The CER indicates the ability of species to predominate in plant communities. The ecological optimum refers to the most favorable combination of ecological factors. The center of the HER refers to the most probable ecological optimum

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\* Corresponding author: probatova@ibss.dvo.ru

if interspecific competition would be absent. The CER/HER ratio refers to the effectiveness of ecological adaptation of species. The disposition of the ecological optimum and the center of the ER show the trend of ecological adaptation. It was reported that properties of ER could be useful as indicators of ecological differentiation of taxa in connection with evolutionary processes. Special attention was paid to ERs in species with various ploidy levels. The trend of ER extension with the increase of ploidy and caryological polymorphism in species was revealed. Coenopopulations of species in geographical profiles from the monsoon zone to inland areas show the transformation that probably affects all of the properties of the ER. The continental climate causes the “continentalization” of ecological niches.

**Keywords:** ecological ranges, holoeorange, coenoeorange, ecological niche, vascular plants, Poaceae, invasive species, monsoon zone, Russian Far East

## INTRODUCTION

The plant cover of the Russian Far East (RFE) is greatly influenced by the position of this region in the monsoon climate zone; the periphery of the largest continent is in contact with the largest ocean, giving rise to a coastline of 22,000 km. The monsoon zone covers a considerable part of RFE, which encompasses the Kamchatka Peninsula, Sakhalin, the Kurile Islands, continental areas and coasts, as well as the islands of the Bering Sea, the Sea of Okhotsk, the Sea of Japan, and the Amur River basin (Russian part). Generally, at least a quarter of Northern Asia, from the Lena River in the north-west and Baikal Lake in the south-west to the Pacific Ocean, is covered by vegetation influenced by the ocean (Box et al. 2001; Safronova & Yurkovskaya 2007). The monsoons of the temperate zone manifest themselves most clearly in the southern part of the RFE. Many representatives of the RFE monsoon flora are absent in other regions of Russia. The origin of plant cover in the ecotone of the Pacific regions of the RFE is determined by the intense influence of East Asian monsoons. The heterogeneity of the monsoon climate in different areas of the RFE contributes to the high variability of the plant cover. The monsoon precipitations increase the contrast of the environment by producing critical periods that restrict the functional stability of the plant communities. The monsoon climate induces the formation of adaptive possibilities. The very special sandbank flora and appropriate plant communities in the Amur River basin exist because of the monsoon climate (Probatova & Sokolovskaya 1981b, Morozov & Belaya 1998a, b). The main features of the Amur River basin are floods with great fluctuations of water level mainly caused by monsoon rains, which occur twice in the warm season; the highest flood takes place in late summer (August) due to heavy monsoon rains. The Amur River basin is a unique depository of plant diversity and represents the northern (northeastern, northwestern) limits of the geographical distribution for many species of southern origin, as well as rare and endangered plant species, which are absent anywhere else in Russia. Some of them are thermophile relicts of tropical origin, while some are taxonomic relicts (e.g., *Symphyllocarpus exilis*, *Bothriospermum tenellum*). Several species of the Amur sandbank flora are endemics of the Amur River basin (e.g., *Beckmannia hirsutiflora*, *Glyceria leptorhiza*, *G. amurensis*, *Agrostis sokolovskajae*). In the monsoon zone, the phenomenon of hydrophilous ephemers (e.g., *Dimeria neglecta*, *Coleanthus subtilis*) was revealed (Probatova 2000). The influence of monsoons leads to the increased biodiversity of plant communities

owing to the phenomenon of seasonal and annual ecological addition (Ramensky 1938; Akhtyamov 1998).

The Pacific monsoon is the main factor that affects the processes of florogenesis and coenogenesis, and determines the structure and functioning of ecosystems in the RFE (Pshenichnikov 2003; Galanin & Belikovich 2009). In the delimitation of the temperate East Asian phytogeographical region, A.V. Galanin & A.V. Belikovich (2009) draw its limits according to the Pacific monsoon region; the southern limit of this region coincides with the isotherm of the mean January temperature, which ranges from 0 to +5 ° C. The problems of monsoon climate botany have been discussed in five conferences held in Vladivostok, all of which were organized by the Botanical Garden-Institute FEB RAS (Plants in monsoon climate 1998, 2003, 2007, 2009; Monsoon climate plants 2000).

One of the main features of the zone under consideration is that all of the components of the plant cover, including species, populations and plant communities, exist under permanent environmental changes, high-degree dynamics, and intensity of ecological factors. The monsoon zone is the area of selection for the survival of plant species growing in special conditions. It is of great importance to study the speciation, structure, functioning, and interactions of the various ecosystems. There is a natural research ground for the study of various dynamic processes, including evolution. The problem of monsoon zone biodiversity is connected with species adaptations, speciation and florogenesis, the formation of plant communities, vegetation dynamics, and population structure. The adaptation of plants to the monsoon climate may lead to significant structural alterations of the vegetative organs (Matyukhin & Manina 2007).

The special features of the monsoon zone are clearly manifested on the coasts. Specific characters of coastal plant communities resulted from the specificity of their habitats. One of the main features of the coastal plant cover is a great variability in the structure and composition of plant communities. The coastal plant communities are mixed, chaotic, unstable, unclosed, unordered, and as variable as their composition and structure. They are fragmentary and often occupy restricted areas, forming various combinations in the coastal landscapes. The low floristic diversity, low density of plant cover and low degree of relationships between species are typical features of coastal plant communities. The disturbance and near total destruction of the coastal plant cover results from storms, landslips and other extreme natural effects and sometimes from intensive human impact.

The coastal part of the monsoon zone in the southern RFE is characterized by the highest genetic and coenotic variability of vegetation cover (Morozov & Belaya 2009). Biological plasticity, adaptive abilities, and various ecological ranges prove the conformity of species in the monsoon zone to various natural regimes from oceanic coasts to Inner Asia. For this transitional land-ocean zone, a wide variability of plant communities is common (Schlothgauer 2009).

We proposed to consider the complex botanical problems connected with the land-sea interactions as a special part of botany - Coastal Botany (Probatova & Seledets 1998, 1999; Probatova et al. 2003, 2005). Multiple publications have been devoted to problems of taxonomy, floristics, phytogeography, ecology, plant anatomy and physiology, phytocoenology and nature conservation in the RFE monsoon zone, especially the RFE sea coasts and islands: Seledets (1969, 1970, 1977, 1978a, 1981, 1988, 2000a, b, c, 2003a, 2009a, b, c, 2010), Probatova (1970, 1973, 1974a, b, 1981, 1984, 1997a, b, 2000, 2003b), Probatova & Seledets (1980, 1983, 1996, 1997), Probatova & Buch (1981), Seledets & Probatova

(1981), Borzova et al. (1985), Barkalov et al. (1986), Barkalov (1987, 1998, 2000, 2009), Chubar (1991, 1992, 1994, 1996, 1998), Burundukova et al. (1997), Neupokoyeva et al. (1998), Probatova, Seledets et al. (1998), Gorovoy et al. (1999), Probatova & Rudyka (2000), Barkalov & Eremenko (2003), Probatova & Barkalov (2003), Chubar et al. (2004), Burkovskaya et al. 2005, Barkalov & Yakubov (2007), Takahashi (2009), etc. The ecological and phytocoenotic properties of plants in the RFE monsoon zone have been the objects of our studies since the late 1960s. Many other publications contain results of the cytological studies (chromosome numbers) of plant species in the RFE monsoon zone (Sokolovskaya & Probatova (1968, 1973a, b, 1974), Probatova & Sokolovskaya (1981a, b, 1983, 1984, 1989), Kozhevnikov et al. (1986), Probatova et al. (1984, 1989, 1996, 1998, 2000, 2001, 2003, 2004, 2006, 2007, 2009, 2010), Probatova (1998, 2003b, c, 2008), Probatova & Rudyka (2003), Probatova & Shatokhina (2007). There is a large collection of voucher herbarium specimens (deposited at the VLA Herbarium, Vladivostok) documenting our chromosome studies.

The Latin names of the taxa cited in this chapter and their chromosome numbers are given according to Vascular plants of the soviet Far East (1985-1996) and Flora of the Russian Far East (2006), as well as to Probatova (2007), Tzvelyov & Probatova (2010).

On the seacoasts and islands in the southern RFE (the Primorsky Territory), there are original undersized oak forests (*Quercus mongolica*), various prostrate forests, and shrub plant communities (*Rosa rugosa*, *Artemisia gmelinii*), *Thymus* spp. communities. It is worth noting *Malus mandshurica* as a prostrate life form on coastal rocks, *Taxus cuspidata* on abrupt rocky slopes, *Rosa rugosa* on coastal sands, and various types of plant communities in the spray zone. There are no such plant communities outside of the seacoasts in the RFE. Steppe-like xerophilous vegetation and *Thymus* communities are not rare on rocks, or on the pebbled and rubble grounds of the coastal zone in the RFE. The interactions of the environmental factors are often very intensive and result in unpredictable consequences, making seacoasts the area of paradoxical ecological situations. Thus, many coastal plants sprayed by seawater or periodically flooded at full sea have evident features of xeromorphosis, conditioned by withering winds and soils that poorly retain water. Halophytes occur in the RFE only on seacoasts and rarely on saline grounds because of man's impact. Xerophytic habitats, specific plant communities, and coenopopulations are the special features of the sea coastal areas. In the southern RFE, sometimes the invasions of dry, hot continental winds take place (Petukhova 2003). Considering these facts, it would be possible to compare the coastal flora with the flora of deserts, but in the coastal habitats of the RFE, C-3 species prevail, while C-4 species are more common in arid intracontinental regions. This finding could be explained by a more favorable water regime on the RFE seacoasts (Burundukova et al. 1997; Neupokoyeva et al. 1998).

More than 500 species of vascular plants are found on the RFE seacoasts; the most typical are species of the maritime belt (Seledets 1970). These are typical coastal species that inhabit the shallow water and spray zones, marshes, coastal meadows, coastal rocks, and slopes of marine terraces. The specific characters of the seaside plant cover are the most pronounced in obligate and facultative halophytes, as well as by species that are tolerant of seaside habitats.

The typical seaside vascular plant species in the RFE belong to 63 genera from the following families: *Alliaceae*, *Apiaceae*, *Asteraceae*, *Boraginaceae*, *Campanulaceae*, *Caryophyllaceae*, *Chenopodiaceae*, *Crassulaceae*, *Convolvulaceae*, *Cupressaceae*, *Cyperaceae*, *Fabaceae*, *Juncaceae*, *Juncaginaceae*, *Lamiaceae*, *Limoniaceae*, *Papaveraceae*,

*Plantaginaceae*, *Poaceae*, *Primulaceae*, *Rosaceae*, *Ruppiaceae*, *Scrophulariaceae*, *Zannicheliaceae*, and *Zosteraceae*. The most numerous families of seaside vascular plants in the RFE are *Poaceae* and *Asteraceae*.

The floristic connections of northeast Asia and North America are distinct on the coastal plant cover in the RFE. The convincing example of such connections is the grass genus *Arctopoa*. The area of distribution of its most ancient species, *A. eminens*, a coastal halophyte with primitive features as to morphology, covers a considerable part of the North Pacific coasts; however, its populations (not numerous) are also represented on the Atlantic coast of Canada (Labrador). In addition, *Arctopoa* spp. are a "connecting link" between the floras of Siberia and Central Asia (Probatova 1974b, 1995a, 2003b). The close relationships become apparent in various taxonomic groups in the RFE and coastal floras of the Korean Peninsula, China, and Japan.

In the land-ocean contact zone, there are limits of geographical distribution for many species of RFE vascular plants. For some species, the area of distribution is located along the seaside, and it is one of characteristic features of this zone. One of the main paths of species migrations occurs along seashores, namely the spray zone, slopes of marine terraces, marshes and wetlands and coastal plains. The regions of the RFE, where the limits of geographical distribution of a number of species occur, show the rich coastal species diversity (Probatova & Seledets 1999).

The specificity of the flora in seacoasts and islands is determined by species connected with the North Pacific area, e.g. *Carex macrocephala*, *Rosa rugosa*, *Leymus mollis*, *Arctopoa eminens*, and *Poa macrocalyx*. Species of northwestern Pacific distribution (Pan-Japan Sea area including) are the most typical and numerous among the RFE coastal vascular plants. The halophytic coastal floristic complex of the RFE contains some groups connected with floras of arid intracontinental regions. The genera of *Poaceae* that are common for arid regions of Russia (e.g., *Stipa*, *Leymus*, *Koeleria*, *Hordeum*, *Agropyron* and *Elytrigia*) are poorly represented (only 1 to 3 species) in the RFE humid climate. Moreover, species of some of these genera are often confined to the seacoasts; examples include *Leymus mollis*, *L. villosissimus*, *Koeleria ascoldensis*, *K. tokiensis*, *Hordeum roshevitzii*, *Arundinella hirta*, *Festuca vorobievii*. In the Primorsky Territory (south of RFE), some coastal species of xerophytic genera such as *Thymus* (e.g., *Thymus ternejicus*) and *Limonium* (*L. tetragonum*) are also mentioned. Some of our data confirm that the species of coastal flora of the RFE, found out of the seacoasts, reflect the ancient status of land-ocean interactions. The limestone paleoreefs occur in southern RFE, and they are characterized by peculiar calcifilous flora. Isolated relict populations of coastal plants are found in the RFE monsoon zone at a considerable distance from the sea shore: *Koeleria tokiensis*, *Festuca vorobievii* and *Arundinella hirta* - on the Lozovy (Chandalaz) Ridge (in the east of Primorsky Territory), *Thermopsis lupinoides* - on the extreme south of the Kamchatka (lakesides of Kurilskoye Lake) and in the southwest of Primorsky Territory (Khanka Lake), *Arundinella hirta* and *Dracocephalum charkeviczii* are found along the Razdol'naya (Suifun) River and *Carex kobomugi* - on the lakeside of Khanka Lake.

The contact land-ocean zone is a natural testing area for many species of intracontinental origin, when they reach seacoasts in the process of their expansion. New habitats are forming continuously on the seacoasts under environmental stress conditions. Speciation is most probable where unoccupied ecological niches occur; these are zones with the most diverse habitats. The phenomenon of isolation of the monsoon populations of intracontinental species

is typical of seacoasts. In recent times, more data have been obtained showing that many genera of vascular plants are represented on the seacoasts by special ecotypes. In a number of genera in RFE (*Dracocephalum*, *Dianthus*, *Adenophora* and *Thymus*), a distinct isolation of coastal races of more or less widely distributed intracontinental species is revealed. The fact that the coastal floristic complex exists proves seacoasts to be a zone of natural selection of populations with higher biological potential (Probatova 1995b, Probatova & Seledets 1999). A large number of coastal species have long been known from the North Pacific coasts, e. g., *Koeleria ascondensis*, *Poa almasovii*, *P. kamczatensis*, *P. macrocalyx*, *P. tatewakiana*, *Setaria pachystachys*, *Artemisia littorcola*, *Arundinella hirta*, *Plantago camtschatica*, *P. japonica*, *Deschampsia macrothyrsa*, *Puccinellia kurilensis*, *P. geniculata*, *P. nipponica*, *Honckenya oblongifolia*, *Salsola komarovii*, *Atriplex subcordata*, *Astragalus marinus*, *Mertensia simplicissima*, *Senecio pseudoarnica*, *Chorisis repens*, *Rosa rugosa*, *Leymus mollis*, *L. villosissimus*, *Heteropappus saxomarinus*, *Calamagrostis deschampsoides*, *Arctopoa eminens*, *Carex macrocephala*, *C. kobomugi*, *C. pumila*, *Ligusticum hultenii*, *Glehnia littoralis*, and *Scrophularia grayana*. The following new coastal species were described in last decades: *Poa vorobievii*, *P. zhirmunskii*, *P. verae*, *P. dudkinii*, *Festuca vorobievii*, *Hierochloë helenae*, *Dracocephalum charkeviczii*, *Thymus ternejicus*, *Adenophora probatovae*, and *Dianthus stepanovae*. There are also coastal ecotypes of widely distributed intracontinental species e.g., *Festuca rubra*, *Potentilla fragarioides* and *Platycodon grandiflorus*.

The specific feature of coastal and island flora of the RFE monsoon zone is a large number of diploid species (2x). According to our studies (Probatova et al. 2003, 2007; Probatova 2007), almost all typical representatives studied of the flora of the monsoon zone in Sakhalin, the Kuriles and the islands of Peter the Great Bay in Primorye (the Sea of Japan) are of low ploidy levels (2x, 4x), proving their relatively low biological potential and high vulnerability.

## MATERIALS AND METHODS

Our studies in the RFE monsoon zone produced the original floristic, caryological, ecological and phytocoenological data that are under consideration here. We evaluated the paths of adaptation to the RFE monsoon zone in various taxonomic groups, as well as the special features of vegetation cover dynamics, and the conditions and the results of species cohabitation in the contact land-sea zone. We determined the typical coastal species position in the system of ecological factors to analyze the changes caused by the natural dynamics of plant cover or human impact. The results of our study of the RFE monsoon zone floristic diversity may clarify the processes of florogenesis in northeastern Asia.

Special attention was paid to Poaceae species represented in the flora of the RFE. The Poaceae can be taken as a model family in floristic and florogenetic studies for the regions where it has a leading position in the floras. The Poaceae family is rich in representatives in the RFE and takes the second place among the largest families in the vascular flora of the RFE, totaling 472 species (excluding the cultivated species) from 91 genera (Probatova 2007). The Poaceae component of the flora of the RFE is characterized by the significant diversity of its composition. The richness of Poaceae diversity in the RFE is conditioned by

the position of this region on the continental edge; the island floras of the RFE are significantly poorer in the Poaceae, but on the islands, some taxa occur that are absent in the continent. Thus, the *Bambusoideae* (*Sasa*), *Brylkinia*, *Moliniopsis*, *Stenofestuca* and *Brachypodium* occur only in South Kuriles and Sakhalin. The special features of Poaceae in the RFE are influenced by the Pacific monsoons, a very special hydrological regime (the Amur River basin) with two floods (in spring and summer), a predominant mountain relief (75% of RFE territory), and volcanic activity. The humid East Asian and Beringian florogenetic centers were the first to form Poaceae flora on the northeastern edge of Asia. The indigenous part of the RFE Poaceae consists of East Asian elements (ca. 41%); about 50% of the indigenous Poaceae species occur in Russia only in the RFE. The following genera of Poaceae are represented in the RFE monsoon zone but are absent in other regions of Russia: *Dimeria*, *Hemarthria*, *Miscanthus*, *Moliniopsis*, *Neomolinia*, *Sasa*, *Stenofestuca*, *Torre-yochloa* and *Zoysia*. Endemic species occur in the monsoon zone of the RFE in areas of intensive volcanic activities on Kamchatka, the Kuriles and Sakhalin. Some examples are *Poa shumushuensis*, *P. kronokensis*, *P. sugawarae*, *P. uzonica*, *Deschampsia tzvelevii*, *Agrostis pauzhetica*, *A. kamtschatica*, *Puccinellia sublaevis* and *Glyceria voroschilovii*. In the Sikhote-Alin Ridge, especially on its east (coastal) mountainside the endemic species *Agrostis sichotensis*, *Calamagrostis latissima*, *C. tataniae* and *Poa sichotensis* occur, while in Lower Amur, the species *Agrostis sokolovskajae* and *Festuca amurensis* are found. From the southern coast of the Sea of Okhotsk, *Poa almasovii*, *P. golubii* and *P. koniensis* have been described (Probatova 2004, 2006).

A comparative ecological study includes different methods, among which are the instrumental measurements of environmental characteristics, studies on habitats and plant communities and phytoindication. Our study is based on the method of ecological scales proposed by L.G. Ramensky (1910, 1938, 1971), who elaborated his individualistic concept of vegetation cover organization before H.A. Gleason (1917, 1924). The method of ecological scales is one of the branches of phytoindication.

The Ramensky method of ecological evaluation of lands was proved very efficient. Based on his method of ecological scales, Ramensky applied the principle of coordination of the characteristics of plant cover with the parameters of the main environmental factors. The comparison of the environmental evaluation in grades of ecological scales with analogous assessment of the tolerance limits allows for a high degree of formalization of the method without laborious experimental studies. At the same time, the method seems to be all-sufficient; the results obtained by its application may be interpreted without involving concepts from adjacent fields of biology. In particular, the simplicity of the method, as well as the seeming possibility of the objective evaluation of the state of the ecosystems, likely implies this method be generally recognized (Prilutzky 2007).

The method of ecological scales was developed for Eastern Europe (Ramensky et al. 1956) and other regions of Eurasia (Tsatsenkin 1967, 1970; Ramensky, Tsatsenkin 1968, Tsatsenkin & Kassach 1970; Tsatsenkin et al. 1974, 1978; Sobolev 1971, 1975, 1978). This method was modified by V. P. Seledets for the RFE monsoon zone. Then the regional ecological scales were elaborated (Seledets 1975, 1976a, b, 1977, 1978a, b, 1980, 1982, 1985, 2000a, b, c, d).

The ecological studies include various directions, some of which revealed the reactivity and sensitivity of species to ecological factors (Ipatov & Kirikova 2001), the plant species

position in vegetation cover (Cheremushkina 2002) and the application of regional ecological scales for classification of vegetation (Komarova et al. 2003).

We consider the problem of plant cover in the monsoon zone at three levels: the regional level (the RFE monsoon zone), the subregional level (the seaside zone, up to the nearest mountain ridges including the islands), and the local level (seacoast vegetation of the maritime belt). We obtained the most detailed data concerning the RFE monsoon zone on subregional and local levels.

The environmental conditions in the monsoon zone are greatly variable and are characterized by very different ecological regimes. Plants that occur in seashores on specific substrates, such as sand, pebble, or underdeveloped soils, often suffer from permanent stress effects. The main ecological factor in the monsoon zone is humidity.

The method of ecological scales assumes that the most important feature of the plant cover is an ecological conditionality. Regionalization is the mainstream of contemporary phytosociology. This method is applicable in many cases when it is necessary to evaluate some area ecologically based on its vegetation. It makes possible to evaluate different ecological regimes, such as humidity, soil fertility and salinity, granulometric composition of soil, drainage, variability of humidity, soil renewal, shading, and anthropotolerance (intensity of the man's impact). Some explanations are needed for the term "soil fertility and salinity" (SFS), which was proposed by the founder of the ecological scales method, L. G. Ramensky. SFS refers to a spectrum of soils, from the poorest to the rich, very rich and saline. Two environmental factors are connected traditionally: a positive factor (the richness in nutrients) transitions to a negative one (the over-concentration of some "salts"), making the soils unfit for plant existence. In the RFE, the real salinity of soils is rare; it occurs especially in the coastal spray zone. The fertility of soils implies a sufficient concentration of nutrients, though some cases of artificial salinity are caused by chemical agents.

The plant communities were studied during field botanical trips. We have over 4000 stand tables (descriptions of plant communities) that were involved in the study.

The ecological characteristics of the coenopopulations were estimated by means of ecological scales (Seledets 1976a, b, 2000a). The study comprised three stages (Seledets 2003a). The first stage was the compilation of ecological characteristics ("ecological portraits") of the coenopopulations, taking into account the complexity of ecological factors that were measured in the grades of ecological scales, namely humidity ("H" scale), soil fertility and salinity ("SFS" scale), anthropotolerance ("A" scale), granulometric composition of soils ("GC" scale), drainage ("D" scale), renewal of soil ("R" scale) and variability of humidity. The second stage of the study measured the amplitudes of ecological factors on geographical profiles to identify the ecological factors most responsible for the variability of the coenopopulations in connection with their position in the geographical area of the species. Based on the results of this study, we described and graphically presented the ecological ranges and ecological niches of the coenopopulations (Seledets 2006, 2009a, 2010b; Seledets, Probatova 2007). The third stage of the study consisted of comparisons of the coenopopulations.

Seacoasts and islands of the RFE provide the unique opportunity to reveal the limits of ecological tolerance for many species. The method of ecological scales allows the measurement of the interval of ecological factors that corresponds to the phenomenon "sea coastal flora" in grades. According to our data (Seledets 2000a; Seledets, Probatova 2003a, 2007), the ecological limits of plant species on the RFE seacoasts taken from two main



factors are humidity (H) (62 to 99 grades) and soil fertility & salinity (SFS) (6 to 20 grades). The ecological optima of the typical coastal species are positioned within these ecological limits: *Arctopoa eminens* (H = 78, SFS = 12), *Arundinella hirta* (H = 78, SFS = 12), *Calamagrostis deschampsoides* (H = 77, SFS = 8), *Leymus mollis* (H = 83, SFS = 20), *L. villosissimus* (H = 71, SFS = 9), *Poa macrocalyx* (H = 72, SFS = 14), and *Puccinellia phryganodes* (H = 98, SFS = 19).

Our material comprised descriptions of coenopopulations in geographical profiles from Inner Asia to the Pacific coast. For comparative studies of coenopopulations, two geographical profiles, about 1000 km each, were traced from the north to the south, first in a continental region from the Lower Lena River (Kyussur village, North Yakutia) to Yakutsk city, and second in a typical monsoon zone from Khayilino village (North Koryakia) to Petropavlovsk-Kamchatsky city, south of Kamchatka Peninsula. The comparison was made to examine whether the coenopopulations of the same species differ notably when areas differ considerably. Our aims were as follows: to reveal the trends of coenopopulation variability in different directions (from the Arctic to Inland Asia and from Inland Asia to the Pacific coast) and to reveal the ecological factors responsible for the ecological variability of the coenopopulations in connection with their position within the geographical area of the species. We studied the ecological properties of coenopopulations, mainly in Poaceae species of the genera *Agrostis*, *Arctagrostis*, *Arctophila*, *Bromopsis*, *Calamagrostis*, *Danthonia*, *Deschampsia*, *Elymus*, *Elytrigia*, *Glyceria*, *Festuca*, *Helictotrichon*, *Leymus*, *Melica*, *Phleum*, *Poa*, *Puccinellia*, *Schizachne*, and *Trisetum*.

As a further development of the ecological scales method, we elaborated on the concept of ecological ranges of species (Seledets 2001, 2003a; Seledets & Probatova 2003a, b, 2007a, b).

## THE CONCEPT OF ECOLOGICAL RANGE

The concept of the ecological range (ecorange, ER) of plant species (Seledets & Probatova 2007b) is a further development of the method of ecological scales. It is based on ecological conditionality, which is the principal property of vegetation cover. The ER concept considers a species as a system of coenopopulations. The ER is not a simple sum of ERs of coenopopulations put together, but it is a complicated system in which the processes of integration and disintegration determine the integrity of the species as a main taxonomic unit and its internal ecological diversity as the necessary and sufficient condition for survival in a diverse and changeable environment.

A coenotic population, or coenopopulation (population of a species within plant community), is the basic notion for phytogeography, phytocoenology and plant ecology. We studied coenopopulations taking into account the concept of metapopulation (Hanski 1998, 1999; Bassargin & Vorobyova 2003a, b). The ecological evaluation of coenopopulations was made by the application of ecological scales. The ER of a species is a complex of ERs of its coenopopulations, which cover the geographical area of species.

We proposed (Seledets 2000a; Seledets & Probatova 2007b) the succession-arealogical classification of coenopopulations (Table 1), a concept based on the position of coenopopulations in succession within the area of the species distribution. Twelve types of

coenopopulations were recognized (centrates, peripherates, isolates and endemates), according to the position of the coenopopulation in a successional series of plant communities (climax, successional and pioneer). This classification of coenopopulations was devised primarily for nature conservation problems (Seledets 1985). Furthermore, this classification proved to be applicable for the description of species ER because it reveals the biogeographical and phytocoenological positions of coenopopulations.

Certain relationships between the geographical position of coenopopulations and the properties of ERs have been revealed. Coenopopulations in the central part of the species area of distribution (climax, successional and pioneer centrates) generally have the largest adaptive potential. Peripheral coenopopulations often have very special features and are, therefore, of great evolutionary value. They often manifest rare adaptations, e.g., a small cane, *Scirpus lineolatus*, at its northern limit of distribution (the north of Primorsky Territory) is able to exist completely under water for a long period of time. Peripheral coenopopulations (climax, successional and pioneer peripherates), as well as isolated coenopopulations (climax, successional and pioneer isolates), are usually impoverished genetically, and their adaptive potential is low. Endemic coenopopulations (climax, successional and pioneer endemates) are of great evolutionary interest and are valuable as nature protection. Our classification is applicable to finding the most favorable type of protected wildlife areas for certain coenopopulations.

We believe that the concept of species ER would be applicable for ecological studies on coenopopulations, species, genera, and in principle, at every taxonomical level. The ER is part of multidimensional ecological space (MES). The ER of a species takes a certain position in the system of ecological coordinates, which includes the humidity, richness/salinity of soil, variability of humidity, granulometric composition of the soil, drainage, and tolerance of human impact. Speciation is the most probable in free ecological niches.

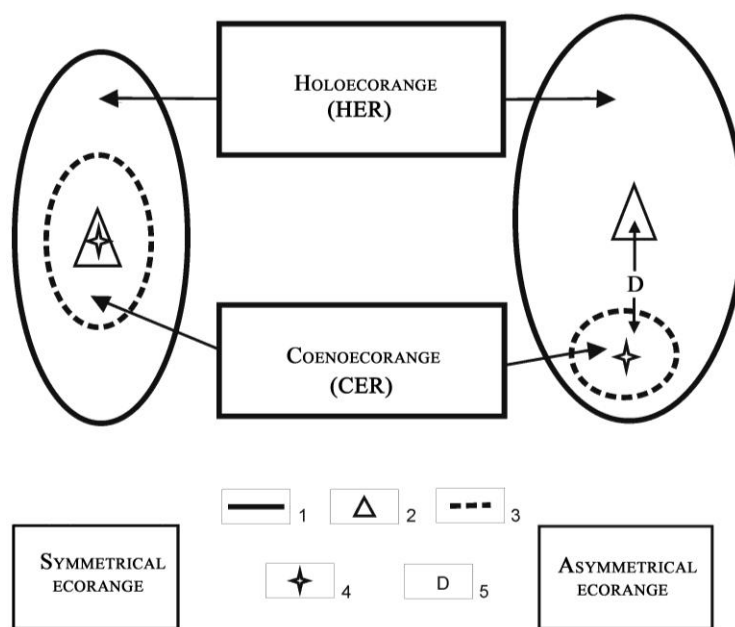
The ER is characterized (Figure 1) by the dimensions, configuration and orientation between the axes of ecological factors; by the definite position in the MES; by the ER of presence, the holoecorange (HER), which is a part of ecological space, where the species is able to exist; by the ER of dominance, the coenoecorange (CER), where the species is the most effective, being the dominant of plant community; by the relationship between them, the CER/HER ratio, i.e., the effectiveness of a species in its ER; and by the ecological optimum and the center of the HER (which coincide in some cases, called symmetrical ER, or in other cases, do not coincide, called asymmetrical ER).

Every species has its own ER, which is an important component of a complex characterization of a species. From the ER, we can determine the taxonomical position of the species, evolutionary trends, peculiarities of geographic distribution, adaptation of species to environmental conditions and position of coenopopulations in plant communities. The ER indicates the conditions under which the species exists. Plant species are not equally tolerant of ecological factors in different parts of the field (Ipatov, Kirikova 2001). The study of ER structure is important when we have to estimate the species' tolerance to environmental factors. Trends of development of the ER show the most probable directions of ecological specialization, which may be a tool for estimating the ecological potential of species.

The concept of ER of plant species incorporates the phytocoenological, biogeographical and evolutionary aspects. The ER, as well as geographical distribution, is a historical phenomenon.

**Table 1. Classification of coenopopulations**

Position of coenopopulations in the species geographic areal	Position of coenopopulations in the plant cover		
	Climax communities	Serial communities	Pioneer groups
Endemate	Climax endemate	Serial endemate	Pioneer endemate
Isolate	Climax isolate	Serial isolate	Pioneer isolate
Peripherate	Climax peripherate	Serial peripherate	Pioneer peripherate
Centrate	Climax centrate	Serial centrate	Pioneer centrate



- 1- limits of the holoecorange
- 2- center of the holoecorange
- 3- limits of the coenoecorange
- 4- ecological optimum (center of the coenoecorange)
- 5- distance between the center of holoecorange and the ecological optimum (in grades of ecological scales)

Figure 1. The structure of ecorange.

The indicative meaning of different features of the ER is provided below.

**Dimensions of the ER (Figure 2)**

The dimensions of the ER define the ecological plasticity of species, i.e., their ability to survive under diverse environmental conditions. The ER dimensions are important because they potentially describe the ecological niche. When we take into consideration three or more

ecological factors, this is the ecological niche. It would be incorrect to consider the ecological niche as a constant property of the species; under certain environmental conditions, the ecological niche may change (Prilutzky 2007). The ecological niche may be described graphically and measured in grades of MES. The dimensions of the ER indicate whether the taxon belongs to an evolutionarily advanced or to a regressive taxonomic group. The species in evolutionary advanced groups are generally characterized by large ERs. Therefore, a large ER indicates a progressive species. *Poa annua* is almost cosmopolitan, and its ER is very large; this species is likely to exist in various environmental situations.

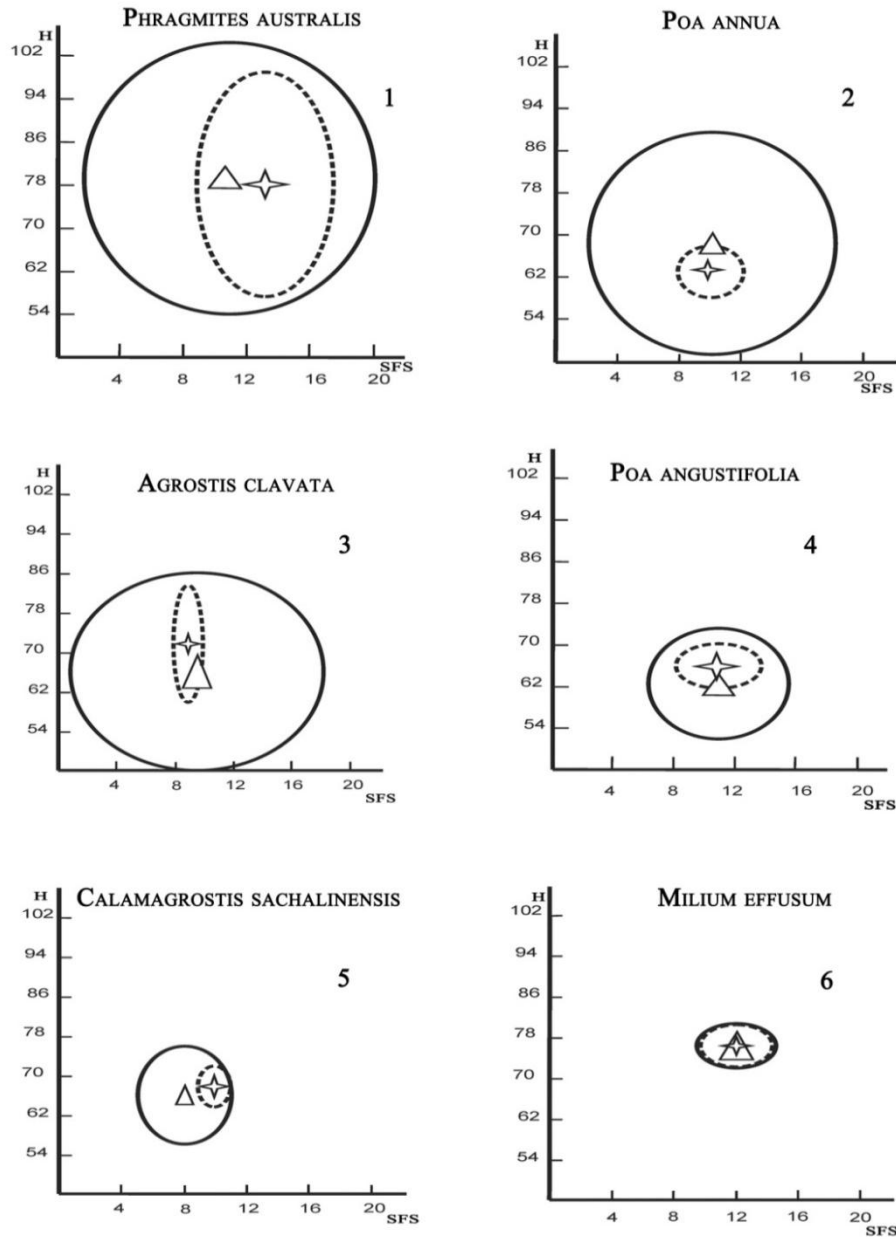


Figure 2. Dimensions of the ecoranges: large - 1, 2, 3; middle - 4, small - 5, 6.

### Configuration of the ER

The configuration of the ER indicates the trend of ecological adaptation of a taxon. The ER may be stretched along one of the ecological axes, and its shape may vary (round, oval, elliptical, etc.).

### Position of the ER (Figure 3)

The position of the ER in the MES shows the area of the active ecological adaptation of a taxon. There is considerable diversity of the ER positions in the MES.

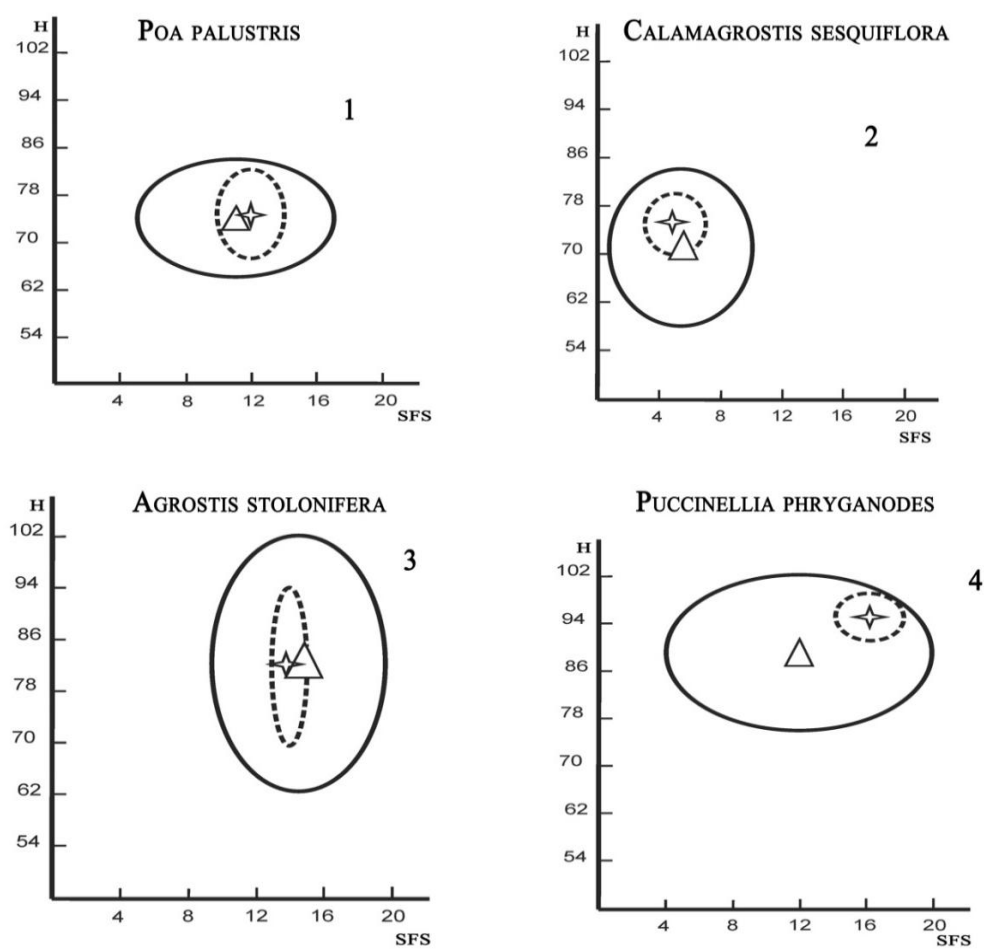


Figure 3. Position of the ecoranges in the field of ecological factors: 1 - central, 2, 3, 4 – peripheral.

### Orientation of the ER (Figure 4)

The orientation of the ER between the axes of ecological factors shows the area of development of the ER in MES. The analysis of the orientation of the ER in the MES can determine the trends of the evolutionary process in various taxonomic groups.

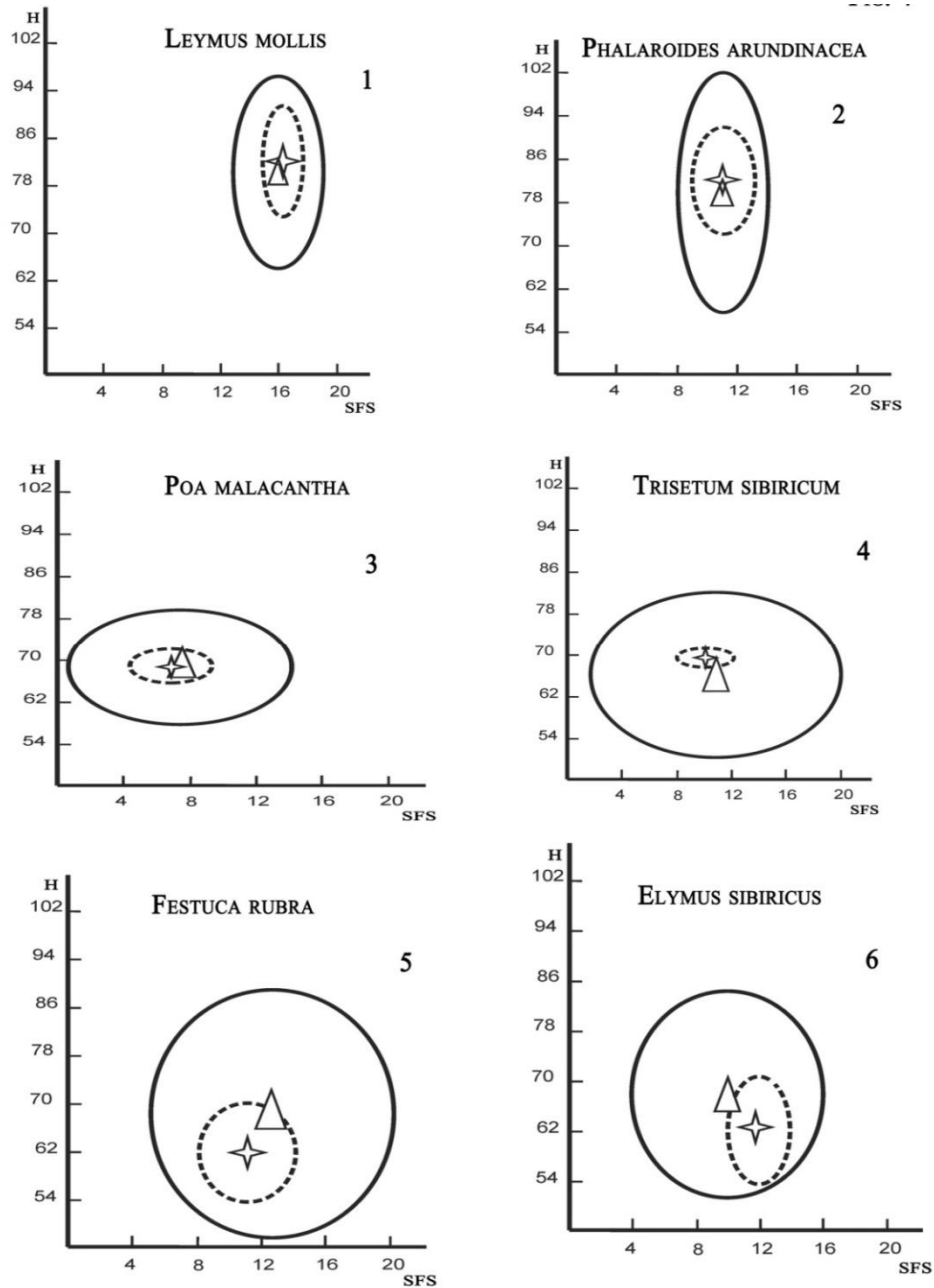


Figure 4. Configuration of the ecoranges: 1, 2 - vertically orientated, 3, 4 - horizontally orientated, 5, 6 - bilaterally orientated.

### Holoecorange (Figure 1)

The holoecorange (HER) reveals the ability of taxa to occupy a certain part of the MES.

### Coenoecorange (Figure 1)

The coenoecorange (CER) shows the ecological regime necessary for the species to dominate in plant communities.

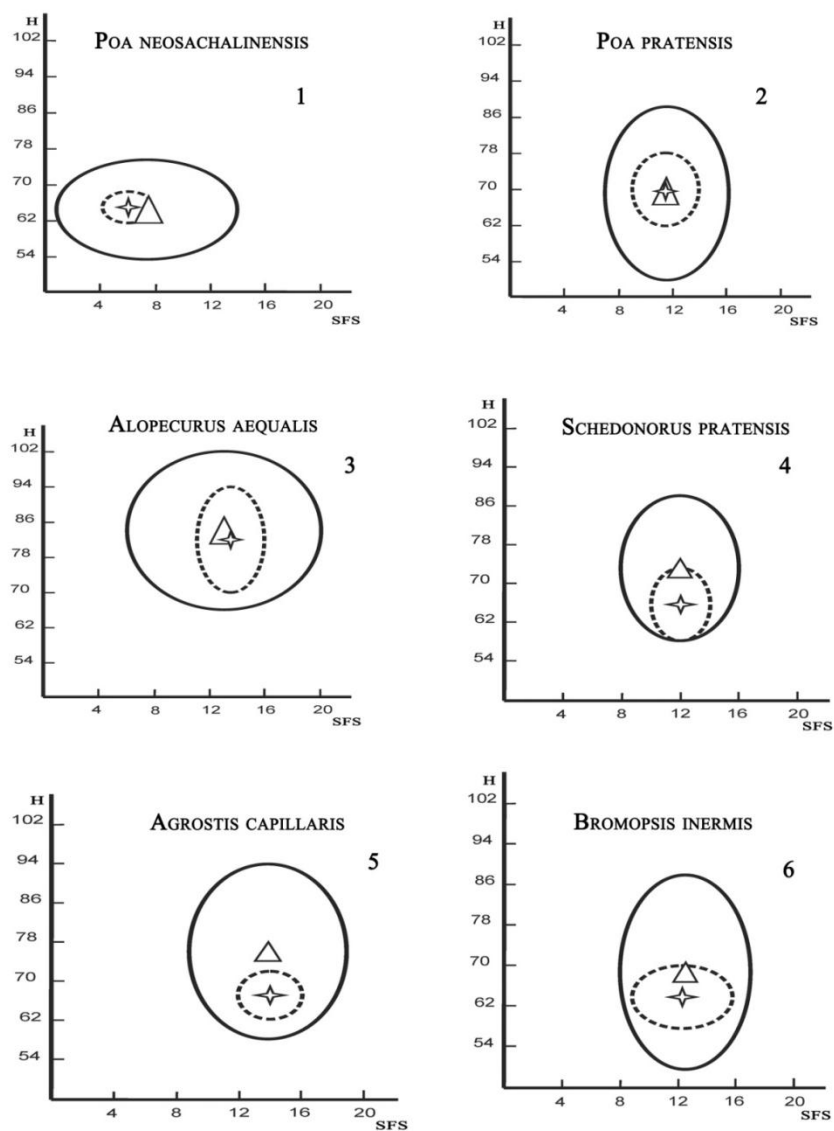


Figure 5. Disposition of the centers of holoecorange and coenoecorange (ecological optimum): close - 1, 2, 3; far - 4, 5, 6.

**Ecological Optimum (See on Figures 2-4)**

The ecological optimum is the point in the species ER where the most favorable combination of ecological factors exists.

**Center of the HER (See on Figures 2-5)**

The center of the HER is the most probable (theoretical) ecological optimum if interactions among species are excluded. The phytocoenotic relationships result in the separation of the ecological optimum and the center of the HER. The degree of separation might be the basis for determining the scale for evaluating the coenotic power of the species, i.e., their ability to dominate in plant communities.

**Distance between the Ecological Optimum and the Center of HER (Figure 5)**

The distance between the ecological optimum and the center of the HER shows the direction of the ecological adaptation of a taxon. The coenotic relationships between species lead to the divergence of the ecological optimum and the center of the HER. The more intensive the competition in the plant community, the more this divergence is pronounced.

**Symmetry of the ER (Figure 1)**

The symmetry of the ER refers to the ecological optimum and center of the HER coinciding.

**Asymmetry of the ER (Figure 1)**

The asymmetry of the ER refers to the non-coincidence or gap between the ecological optimum and the center of the HER. We consider asymmetry of the ER to be the evidence for the primary stage of species adaptation to a new habitat.

**Effectiveness of the Species in the ER (Figure 6)**

The effectiveness of the species in the ER (CER/HER ratio, %) refers to the degree of ecological adaptation of species. It provides information about the role of a species as a component of plant communities. The highest degree of effectiveness occurs when the species dominate throughout almost all ER. A completely effective ER occurs when the HER and the CER coincide, but such species are scarce; far more species are approaching this state. The degree of this approach may be measured because when the CER/HER ratio is higher, the ER effectiveness is higher as well.



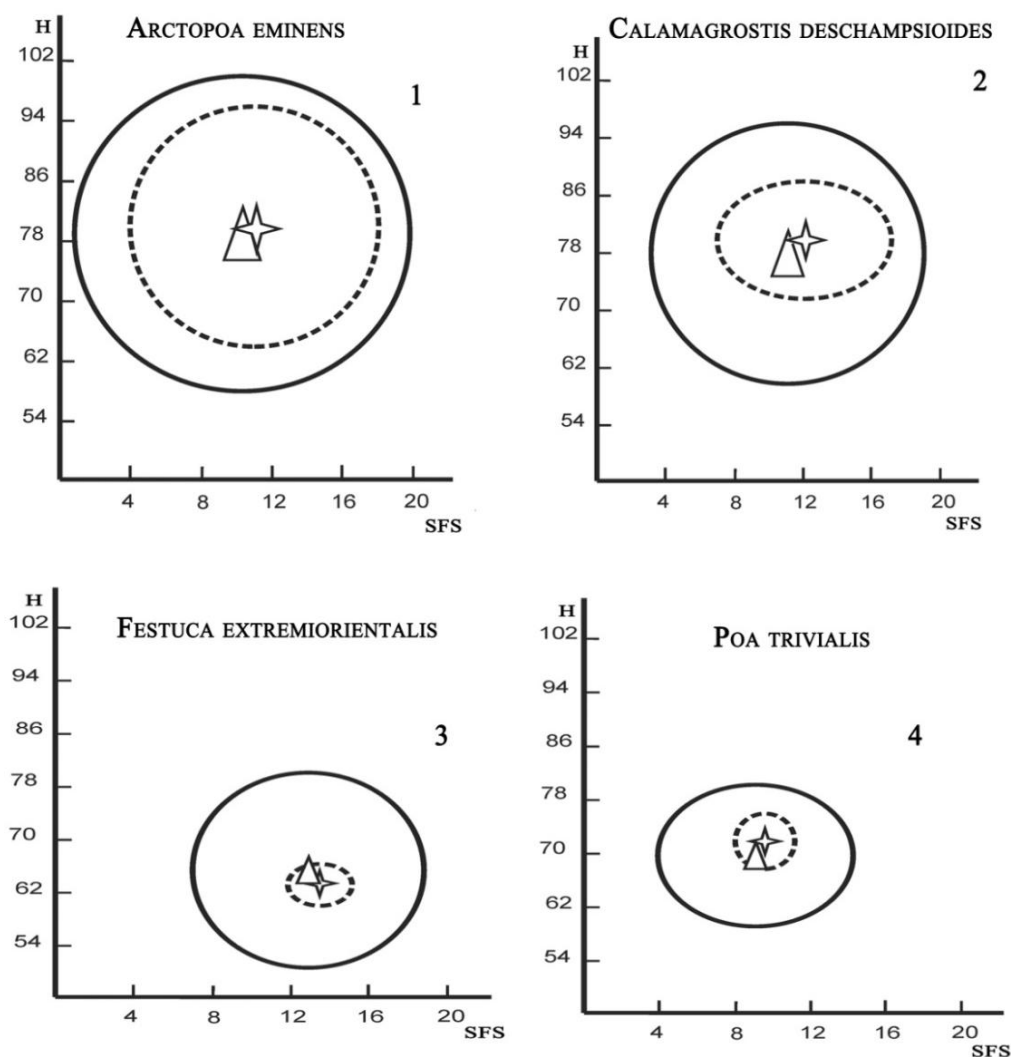


Figure 6. Effectiveness of the species in the ecorange: high - 1, 2; low - 3, 4.

The meaning of "ER dimensions" may be illustrated by the RFE Poaceae species with different ploidy levels. Connections between the ER dimensions and the position of coenopopulations of species within the area of distribution were demonstrated. In the Poaceae, the largest ERs are found in diploid successional centrates (e.g., *Beckmannia syzigachne* and *Trisetum sibiricum*,  $2n = 14$ ). The second group of species with a large ER are diploid successional peripherates (e.g., *Bromopsis canadensis*,  $2n = 14$ ). Differences in the structure of the ER within these groups are considerable. In the first group of species, the centers of the HER (ecorange of existence) are considerably far from the centers of the CER (ecorange of dominancy). In the second group, the centers of the HER and CER are very close. Thus, the peripherates may be in their optimal habitats.

Tetraploid (4x) species are represented by environmentally tolerant coenopopulations (e.g., *Calamagrostis sesquiflora*, *Agrostis stolonifera* and *Leymus mollis*,  $2n = 28$ ). A similar situation was observed for species with higher or variable ploidy levels. The effectiveness of

the ER increases from endemates (*Poa neosachalinensis*, 6x-9x, 2n = 42-63) to centrates (*P. angustifolia*, 2n = 56-64; *P. macrocalyx*, 2n = 42-c.100) and periferates (*Calamagrostis sachalinensis*, 4x-8x, 2n = 28-56). Thus, the effectiveness of the ER is connected to the ploidy levels, especially with variable ploidy, and the position of coenopopulations within the geographical area.

The coincidence of ecological optimum and the center of the HER is typical for successional peripherates (*Festuca extremiorientalis* and *Milium effusum*, 2n = 28), and the same is true for successional centrates (*Poa annua* and *Trisetum spicatum*, 2n = 28). In some peripherates, the ecological optimum is far from the center of the HER (*Agrostis stolonifera*, 2n = 28). As a rule, it is also far in climax centrates (*Calamagrostis sesquiflora*, 2n = 28) and successional centrates (*Poa palustris*, *Leymus mollis*, *Calamagrostis deschampsoides*, *Phalaroides arundinacea* and *Elymus sibiricus*, 2n = 28).

The relationships of the species with genetic variability and ecological properties became a special field of botanical studies (Grant 1963; Tateoka 1973; Bebbel & Selander 1975; Gray et al. 1979; Ehrendorfer 1980; Stebbins 1984; Rothera & Davy 1986; Bayer et al. 1991; Brochmann & Elven 1992). Polyploidy is considered a major evolutionary process in flowering plants and has attracted much research time and effort; thus, ecological studies will make substantial contributions concerning the evolution of polyploidy (Bayer 1998). The adaptive significance of polyploidy is that it may allow polyploids to occupy niche space not occupied by diploids. Polyploid complexes are very dynamic, often rapidly evolving, systems.

The typical species from the southern RFE monsoon flora commonly studied have comparatively low ploidy levels (Seledets & Probatova 1989; Probatova, & Rudyka 2000; Probatova et al. 2003, 2007, etc.), e.g., *Artemisia keiskeana*, *Pterocypsela raddeana*, *Lamium barbatum*, *Carpinus cordata*, *Aster maackii*, *Dioscorea nipponica*, *Agastache rugosa*, *Amphicarpaea japonica* (all - 2x), *Sisymbrium luteum* and *Phryma asiatica* (both - 4x). Our studies showed that the ecological amplitude of polyploids is generally much broader than that of diploids. However, on the RFE seacoasts, diploids dominate (over 50% of the species studied), especially among halophytes, proving this floristic complex to be ancient (Probatova et al. 1984, 2003c). The study of environmental factors and caryotaxonomic data in the various groups of coastal vascular plants showed that diploids are more common on infertile coastal soils, but they take a secondary position in plant cover on fertile soils because of competitive relationships. Hexaploids (6x) and species with higher ploidy levels are able to exist in a significantly wider amplitude of ecological factors than species of low ploidy levels. Thus, the ploidy level is an important indicator of the preadaptation of species to ecological stress. In harsh but stable environmental conditions, the diploid level is optimal (specialized taxa). Owing to high ecological plasticity, polyploids take advantage of unstable environmental situations, including human impact. Generally, polyploids in the RFE monsoon zone are characterized by large geographical areas of distribution and ecological amplitude and a high degree of biological potential, which manifests itself as the tolerance to human impact (Probatova et al. 2003c). The ERs in taxa of hybrid origin are larger than ERs of possible ancestral forms (Probatova, Seledets 1999; Probatova 2007; Seledets, Probatova 2007b). Correlations of ERs and ploidy levels in species are especially worth studying.

## ECOLOGICAL DIFFERENTIATION

The problem of ecological differentiation of species is important for plant taxonomists and ecologists. Different types of ecological differentiation show the diversity of vital strategies, various ways of adaptations to habitats and, certainly, different paths of evolution in plant taxonomic groups. We studied this problem on some typical Poaceae groups in the RFE.

Within the genus *Elymus* of the flora of the RFE, three groups of species were revealed according to a combination of ecological factors. According to Tsyganov (1974), the first group includes oligomesotrophic orthomesophytes (*Elymus macrourus* and *E. kamczadalarum*). The second group includes mesoeutrophic xeromesophytes (*E. mutabilis*, *E. jacutensis* and *E. sibiricus*), and the third group includes mesoeutrophic orthomesophytes (*E. gmelinii*, *E. kronokensis* and *E. dahuricus*). This is a linear type of ecological differentiation. In *Arctopoa*, the differentiation of species is clearly manifested; species are located far from one from another along the same axis of humidity. This type of differentiation is also linear. The same situation occurs in *Glyceria*. The ERs of the three species we studied, *G. lithuanica*, *G. triflora*, and *G. spiculosa*, are located on the line in the same axis of humidity.

The second type of ecological differentiation is termed bioriented and refers to two directions of adaptation to environmental factors. This phenomenon can be illustrated by *Calamagrostis* in the RFE, where the change in direction of ecological differentiation takes place. The first group of *Calamagrostis* species evolved from orthomesophytic and orthomesotrophic habitats to xeromesotrophic mesoeutrophic ones (*C. sachalinensis* and *C. brachytricha*). However, the second group developed from the "point of diversification" to hydromesotrophic and mesoeutrophic habitats (*C. lapponica*, *C. langsdorffii* and *C. neglecta*). This type of ecological differentiation of species indicates certain trends of evolution in a large taxonomic group. Every line has its own path of environmental adaptation.

In *Agrostis* of the RFE, the ecological optima of species in the *Agrostis* section are oriented along the "humidity" axis, while in the *Trichodium* section, they are oriented diagonally (just between the "humidity" and "richness-salinity" axes). The latter is the third, or diagonal, type of ecological differentiation.

The ecological differentiation of species is more complicated in the genus *Poa*, the largest genus among Poaceae of the flora of the RFE. Every section of this genus has its own type of ecological differentiation. Species of the section *Poa* (s. str.) are mostly mesophytes, while species of section (former subsection) *Malacanthae* occur in orthomesophytic and orthomesotrophic habitats. This difference may prove the validity of separation of *Malacanthae* group, which is mainly the North Pacific, from the section *Poa* in its former sense (Probatova 2007). The comparative age of some closely related species may be determined by the degree of their ecological differentiation.

One of the basic problems of phytogeography, ecology, and phytocoenology in the contact land-ocean zone is to discover how plants overcome the ecotone of the global scale: the transition from continental Asia to the Pacific Coast. Regularities of the transformation of taxonomical composition of plant communities from the seaside to inland in the monsoon zone were described for the Kamchatka Peninsula since V.L. Komarov (1937); later, many authors studied this phenomenon in detail (Plotnikova & Trulevich 1974; Stepanova 1985, Neshatayeva 1988; Kravchunovskaya et al. 2008, 2009, etc.).

The variability of the ERs of the coenopopulations in the transitional land-ocean zone is a new field of study. We compared the Yakutian and Pacific coastal geographical profiles. In the intracontinental subregions, the dimensions of the ERs of the coenopopulations reflected the grades of continentality. It has been discovered that the ecological optima of many coenopopulations in coastal areas are located in more humid conditions when compared to intracontinental areas. This finding suggests the adaptation of coenopopulations in coastal and intracontinental areas occurred in different ways. While migrating from intracontinental subregions to coastal ones, the species produce various coastal ecotypes.

The ecological orientation of the coenopopulations is different in intracontinental and coastal areas. The intracontinental populations are orientated mainly along the "humidity" axis, but coastal ones are found along the "fertility-salinity of soils" axis. Thus, the ecological properties of the coenopopulations depend on their geographical position.

The largest ERs of the coenopopulations were discovered in Central Yakutia, and the small ones were in the Lower Lena River basin. On the Pacific Coast, there are not great differences between the northern and southern coenopopulations. Sometimes they are almost equal in the northern and southern RFE. For instance, in some species in the North Koryakia the ERs of coenopopulations were of almost the same dimensions as in the extreme south of the Kamchatka Peninsula.

We showed the phenomenon of decreasing the ERs of coenopopulations when moving from areas with optimal ecological conditions to less favorable ones, if the continental plant species migrate from Inner Asia to the Pacific Coast. The ERs of coenopopulations decrease considerably when moving from the center toward the limits of the geographical range of plant species. The study of coenopopulations in Yakutia and the Pacific coastal areas of the RFE led us to the following conclusion: the ecological and phytocoenological positions of plant species are determined mainly by the humidity and fertility-salinity of soils.

In intracontinental regions, the ERs with a high degree of effectiveness are common (e.g., in *Calamagrostis purpurascens*, *Festuca altaica* and *Helictotrichon krylovii*) and show high specialization. In the coastal regions, mostly asymmetrical ERs are typical and indicate a low degree of ecological specialization. Symmetrical ERs are more common in species of continental Asia; the majority of species studied in the Pacific Coast have more or less asymmetrical ERs. Species of Inner Asia use their ER more efficiently than the majority of species in the Pacific Coast of the RFE.

We compared the coenopopulations of the typical North Pacific coastal species *Leymus mollis*, which was studied at Sakhalin and on the seashore of the continental part of Primorye (Seledets 2009a). It was discovered that in the continental area, the ecological niche of *L. mollis* is distinctly larger than on the island, i.e., the maximal value of almost all factors in Primorye are more significant than in Sakhalin.

Depending on the phytocoenology of the species, the regularities of the ER changes may be more or less distinct (Seledets 2003b, 2004, 2009c; Mayorov et al. 2009).

The definition of ecological niche at the limits of the species' geographical distribution is one of the most important problems of contemporary biogeography. Taking into account the main ecological factors, we studied the transformation of the ecological niches of *Agrostis trinii*, a mainly inland (Siberian) species (of dry meadows), and *Calamagrostis brachytricha*, a species typical of the East Asian monsoon zone (forest edges on the slopes). Their ERs were studied in inland areas, on the islands (Peter the Great Bay) and on the coasts of southern Primorye, where both of the species are at the limits of their areas of distribution. The ERs of

species in the Pacific coast of the RFE differ from ERs of the same species in continental areas by many features, namely the dimensions, position in MES, configuration, orientation along certain axes of ecological space and CER/HER ratio. We propose to term this phenomenon as the "continentalization of ecological niche". The transformation of the ecological niches of the species may be one of the ways to overcome the transitional land-ocean zone.

The ER may be considered a resource of invasive activity (Table 2, Figure 7). Invasive species (alien or introduced) are essential and are a constantly increasing component of the floristic diversity in the RFE. We distinguish the three following types of invasion: island invasion, continental invasion and regional invasion (Seledets 2010a).

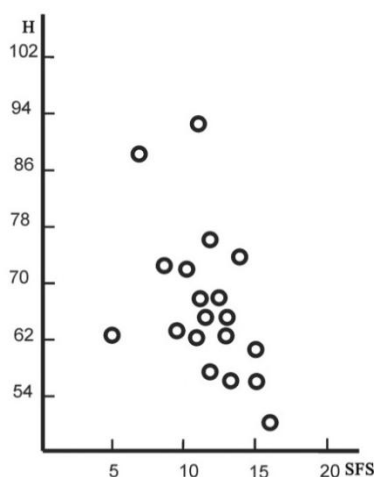


Figure 7. Ecological optima of the Poaceae species, invasive in the Russian Far East.

**Table 2. Description of ecoranges (in grades of ecological scales) of the species, invasive in the Russian Far East**

Species	Ecological optimum		Extension of ER		Dimensions of ER
	H	SFS	H	SFS	
<i>Agrostis gigantea</i>	81	11	50	15	750
<i>A. capillaris</i>	63	12	32	9	288
<i>Alopecurus arundinaceus</i>	73	13	50	10	500
<i>A. pratensis</i>	72	14	30	13	390
<i>Anthoxanthum odoratum</i>	66	9	25	5	125
<i>Bromopsis inermis</i>	63	13	40	9	360
<i>Dactylis glomerata</i>	63	10	20	8	160
<i>Leymus chinensis</i>	56	12	13	6	78
<i>Phleum pratense</i>	68	12	34	12	408
<i>Poa annua</i>	65	7	61	14	854
<i>P. trivialis</i>	72	10	15	10	150
<i>Schedonorus pratensis</i>	66	11	27	6	162

Note. H - humidity, SFS - soil fertility & salinity. Dimensions of ER are given in conventional units (H x SFS).

## Island Invasion

The phenomenon of island invasion consists of the successful reproduction of invasive species in the islands, where they occupy new habitats, invade natural plant communities, and expand their distribution area, e.g., *Agrostis capillaris* in Sakhalin (Probatova 1985, 2003a, 2007). *A. capillaris* is completely naturalized in Sakhalin, and according to the properties of its ER, the species is promising for insular territories. The great distance between its ecological optimum and the center of the HER proves this assumption. In the continental parts of the RFE, these species do not occur at all, or they are rare, and there is no reason for their expansion. The most evident feature of the ERs of such species is the low degree of effectiveness (CER/HER).

## Continental Invasion

There are many cases of invasive species in the continental part of the RFE. Nevertheless, most of the species disappear as unexpectedly as they appear. The naturalization of invasive species on the continent is lower than on the islands. The competitive relationships in the continent are tenser. Examples are *Alopecurus arundinaceus*, *Arctopoa subfastigiata*, *Calamagrostis epigeios*, and *Leymus chinensis*. The diversity of the ERs in this group of species is greater than in the group of the island invasion; differences in the dimensions of the ER as well as in the ER effectiveness are considerable.

## Regional Invasion

This situation corresponds to the largest diversity of ecological and phytocoenological situations in the RFE. Species of this group are the most able to invade the plant cover of a new area. Here we list some examples of this type of invasion in the RFE (all of which are polyploids: 4x, 6x, 8x): *Agrostis gigantea*, *Alopecurus pratensis*, *Bromopsis inermis*, *Dactylis glomerata*, *Phleum pratense* and *Poa annua*. The reserve of activity in the group of regional invasion is greater than in the island and continental types. The variability of the ERs in this group is more than in other groups. In some species (e.g., *Phleum pratense* and *Poa annua*), the distance between the ecological optimum and the center of the HER is minimal, meaning that the species exhausted its possibilities of adaptation. In others, the distance is considerable, and these species have asymmetrical ERs (*Agrostis gigantea*, *Alopecurus pratensis*, *Bromopsis inermis* and *Dactylis glomerata*); the potentialities of these species are not yet exhausted.

Studying of ERs allows for the differentiation of the invasive component of the flora according to the type of adaptation of the species to the complex environmental factors. In addition, applying the ER method enables the forecast of the ways and rates of future invasions of species.

## CONCLUSION

All of the parameters of the ecological ranges of the coenopopulations in the intracontinental parts of the species area of distribution differ from those of the Pacific Coast areas. The variability of the coenopopulations also depends on their position in the plant cover. In the geographical profile from Inner Asia to the Pacific monsoon zone, the properties of the ecological ranges change. The relative position of the ecological optimum and the center of the ecological range, as well as the distance between them, show the direction of ecological adaptation of the taxa. The coenotic relationships of the species lead to divergence of the ecological optimum and the center of the ecological range because when the competition in a plant community is more intense, this divergence will be more pronounced. As for the monsoon zone, the considerable transformation of ER occurred according to environmental conditions. Changes in the ecological range are indicators of the evolutionary processes. The study of ecological ranges is one of the ways to assess the evolutionary prospects of the species.

## REFERENCES

- Akhtyamov, M. Kh. (1998). *Monsoons and special features of meadows in south part of the Russian Far East*. In: O.V. Khrapko, (Ed.), *Plants in monsoon climate: Proceedings of the conference devoted to the 50-th anniversary of the Botanical Garden-Institute FEB RAS (3-5)*. Vladivostok: Dal'nauka. (In Russian).
- Barkalov, V. Yu. & Eremenko, N. A. (2003). *Flora of nature reserve "Kurilsky" and nature zakaznik "Malye Kurily"* (Sakhalinskaya Oblast). Vladivostok: Dalnauka., (In Russian).
- Barkalov, V. Yu. & Yakubov, V. V. (2007). New species for the flora of Russia - *Psilotum nudum* (L.) Beauv. (Psilotaceae) from the Kurile Islands. *Bot. Zhurn.*, (St.-Petersbourg), 92, 12, 154-156. (In Russian).
- Barkalov, V. Yu. (1987). *Boehmeria tricuspis* (Urticaceae) – a new species of the USSR flora from the Kurile Islands. *Bot. Journ.*, (Leningrad), 72, 11, 1548-1550. (In Russian).
- Barkalov, V. Yu. (1998). Vascular plants of the Kuril'sky nature reserve (Sakhalinskaya Oblast'). In: A. E. Kozhevnikov, (Ed.), *Flora of protected wildlife areas of the Russian Far East: Magadansky, Bureyinsky and Kuril'sky nature reserves (71-113)*. Vladivostok: Dalnauka., (In Russian).
- Barkalov, V. Yu. (2000). Phytogeography of the Kurile Islands. In: T. Komai, (Ed.), *Results of recent research on Northeast Asian biota. Nat. Hist. Res., Special Issue, 7 (1-14)*. Chiba: Natural History Museum and Institute (Japan).
- Barkalov, V. Yu. (2009). *Flora of the Kuril Islands*. Vladivostok: Dalnauka., (In Russian).
- Barkalov, V. Yu., Kozhevnikov, A. E. & Kharkevich, S. S. (1986). Vascular plants of Verkhoturova and Karaginsky Islands (the Bering Sea) and conservation of their gene pool. *Komarov Memorial Lectures (Vladivostok)*, 33, 110-168. (In Russian).
- Bassargin, D. D. & Vorobyova, A. N. (2003a). Problems of plant population-specific differentiation in the aspect of the Pacific effect. In: S. B. Gontcharova, (Ed.), *Plants in monsoon climate, III: Proceedings of III International conference " Plants in Monsoon Climate."* (198-199). Vladivostok: BGI FEB RAS. (In Russian).

- Bassargin, D. D. & Vorobyova, A. N. (2003b). *Saussurea* (Asteraceae) species in the aspect of "Levins rule". In: S. B. Gontcharova, (Ed.), *Plants in monsoon climate, III: Proceedings of III International conference "Plants in Monsoon Climate."* (199-203). Vladivostok: BGI FEB RAS. (In Russian).
- Bayer, R. J. (1998). New perspectives into the evolution of polyploid complexes. In: *Plant evolution in man-made habitats. Proceedings of VII Symposium of IOPB, Amsterdam*, (359-373).
- Bayer, R. J., Purdy, B. G. & Lebedyk, D. G. (1991). Niche differentiation among eight sexual species of *Antennaria* Gaertner (Asteraceae: Inuleae) and *A. rosea*, their allopolyploid derivative. *Evol. Trends in Plants*, 5, 109-132.
- Bebbel, G. R. & Selander, R. K. (1975). Genetic variability in edaphically restricted and widespread plant species. *Evolution*, (USA), 28, 4, 619-630.
- Borzova, L. M., Klychkova, T. V., Probatova, N. S., Syomkin, B. I. & Kharkevich, S. S. (1985). The rediscovery of the rarest species *Dimeria neglecta* in the Primorsky Territory. *Bot. Journ.* (Leningrad), 70, 9, 1261-1265. (In Russian).
- Box, E. O., You, Hai-Mei, Li, Dong-Liang. (2001). Climatic ultra-continentality and the abrupt boreal-nemoral forest boundary in northern Manchuria. *Studies on the vegetation of alluvial plains* (183-200).
- Brochmann, C. & Elven, R. (1992). Ecological and genetic consequences of polyploidy in arctic *Draba* (Brassicaceae). *Evol. Trends in Plants*, 6, 111-124.
- Burukovskaya, E. V., Burundukova, O. L. & Probatova, N. S. (2005). Structural and functional adaptations of the photosynthetic apparatus in coastal vascular plants - halophytes (southern Russian Far East). In: O.V. Khrapko, (Ed.), *Rhythms and catastrophes impact on the vegetation of the Russian Far East: Proceedings of the International conference "Rhythms and catastrophes impact on the vegetation of the Russian Far East"* (232-238). Vladivostok: BGI FEB RAS. (In Russian).
- Burundukova, O. L., Neupokoyeva, E. V. & Probatova, N. S. (1997). Halophytes on seacoasts of southern Far East: anatomic and physiological aspects of adaptation. In: *Animal and plant life of the Far East*, 3, 210-215. Ussurijsk. (In Russian).
- Cheremushkina, V. A. (2002). Ecological and phytocoenotic position of *Allium* L. representatives in mountain ecosystems of Eurasia. *Sib. Ecol. Journ.* 9, 5, 565-570. (In Russian).
- Chubar, E. A. (1991). New species for the flora of the islands of the Far East marine reserve. *Bot. Zhurn.*, 76, 11, 1620-1622. (In Russian).
- Chubar, E. A. (1992). Addition to the flora of the islands of the Far East marine reserve. *Bot. Zhurn.*, 77, 12, 131-133. (In Russian).
- Chubar, E. A. (1994). Additions and changes to the flora of the islands of the Far East marine reserve. *Bot. Zhurn.*, 79, 7, 128-130. (In Russian).
- Chubar, E. A. (1996). Additions to the flora of the islands of the Far East marine reserve. *Bot. Zhurn.*, 81, 10, 117-119. (In Russian).
- Chubar, E. A. (1998). A find of *Matteuccia orientalis* (Onocleaceae) in South Primorye and new species for the flora of the islands of the Far East marine reserve. *Bot. Zhurn.*, 83, 3, 150-152. (In Russian).
- Chubar, E. A., Probatova, N. S. & Seledets, V. P. (2004). Vascular plants. In: A. N. Tyurin, & Drozdov, A. L. (Eds.), *Far Eastern marine biosphere reserve, II, Biota* (373-420). Vladivostok: Dalnauka., (In Russian).



- Ehrendorfer, F. (1980). Polyploidy and distribution. In: W.H. Lewis, (Ed.), *Polyploidy: Biological Relevance* (45-60). New York.
- Flora of the Russian Far East: Addenda and corrigenda to "Vascular plants of the Soviet Far East", vols. 1-8 (1985-1996). A. E. Kozhevnikov, & N. S. Probatova (Eds.). (2006). *Vladivostok: Dalnauka.*, (In Russian).
- Galanin, A. V. & Belikovich, A. V. (2009). The Pacific monsoon zone: phytogeographical regionalization, plant migrations, and distinctive features of speciation. In: A. V. Belikovich, (Ed.), *Plants in Monsoon Climate V: Proceedings of V Conference "Plants in Monsoon Climate."* (33-43). Vladivostok: Dalnauka., (In Russian).
- Gleason, H. A. (1917). The structure and development of the plant associations. *Bull. Torrey Bot. Club*, 44, 10, 463-481.
- Gleason, H. A. (1924). The individualistic concept of the plant association. *Bull. Torrey Bot. Club*, 53, 7-26.
- Gorovoy, P. G., Chubar, E. A. & Volkova, S. A. (1999). New genus *Limonium* (*Limoniaceae*) in the flora of the Russian Far East and new species *L. tetragonum* in the flora of Russia. *Bot. Journ.*, (St.-Petersbourg), 84, 7, 144-147. (In Russian).
- Grant, V. (1963). *The origin of adaptations*. New York.
- Gray, A. J., Parsell, R. J. & Scott, R. (1979). The genetic structure of plant populations in relation to the development of salt marshes. In: *Ecological processes in coastal environment. First Ecol. Symp. and 19-th Symp. Brit. Soc., Norwich, 1977.* (43-64). Oxford.
- Hanski, I. (1998). Metapopulation dynamics. *Nature*, 396, 41-49.
- Hanski, I. (1999). *Metapopulation ecology*. Oxford.
- In: P. Ya. Baklanov & L. D. Filatova (Eds.), *Geographical studies in the Far East*. Proceedings of the conference devoted to the 150-th anniversary of the Russian geographical society (151-153). Vladivostok: Dalnauka., (In Russian).
- Ipatov, V. S. & Kirikova, L. A. (2001). Reactivity and sensitivity of species to ecological factors. *Bot. Journ.*, (St.-Petersbourg), 86, 3, 80-86. (In Russian).
- Komarov, V. L. (1937). Vegetation of seacoasts in Kamchatka Peninsula. *Transactions of the Far East Branch of USSR Academy of Sciences, Ser. Bot.*, 2, 7-17. (In Russian).
- Komarova, T. A., Timoszenkova, E. V., Prokhorenko, N. B., Aszpekova, L. Y., Yakovleva, A. N., Sudakov, Yu. N. & Seledets, V. P. (2003). Regional ecological scales and their application for classification of the forest vegetation of the Russian Far East. Vladivostok: Dalnauka., (In Russian).
- Kozhevnikov, A. E., Sokolovskaya, A. P. & Probatova, N. S. (1986). Ecology, geography and the chromosome numbers of some Cyperaceae species from the soviet Far East. *Proceedings of the Siberian Branch of the USSR Academy of Sciences. Biol.*, 13, 2, 57-62. (In Russian).
- Kravchunovskaya, E. A., Myalo, E. G. & Sidneva, E. N. (2009). Plant communities of multiple-aged marine terraces in Avachinsky Bay, East Kamchatka. In: A.V. Belikovich, (Ed.), *Plants in the Monsoon Climate. V: Proceedings of V Conference "Plants in Monsoon Climate."* (88-90). Vladivostok: Dalnauka., (In Russian).
- Kravchunovskaya, E. A., Pinegina, T. K. & Sergueyeva, A. M. (2008). Plant communities of multiple-aged coastal banks in Kamchatka. In: *Proceedings of the IX International scientific conference "Conservation of biodiversity of Kamchatka and adjacent seas"* (70-73). Petropavlovsk-Kamchatsky. (In Russian).

- Matyukhin, D. L. & Manina, O. S. (2007). Structural peculiarities of shoots in the species and varieties of *Juniperus* L. originated from the regions with monsoon climate. In: S. B. Gontcharova, (Ed.), *Plants in monsoon climate*, 2006. IV. Proceedings of IV International conference "*Plants in Monsoon Climate.*," (383-384). Vladivostok: BGI FEB RAS. (In Russian).
- Mayorov, I. S., Seledets, V. P. & Probatova, N. S. (2009). Ecoranges of plant species in adaptive zones. *Herald of the Krasnoyarsk State University of Agriculture*, 28, 2, 47-56. (In Russian).
- Monsoon Climate Plants. (2000). II International conference "*Monsoon Climate Plants*". (Abstr.). O.V. Khrapko (Ed.). Vladivostok: Dalnauka., (In Russian).
- Morozov, V. L. & Belaya, G. A. (1998a). Ecological and phytocoenotic positions of steppe meadow plant communities in Primorye and Priamurye. In: O. V. Khrapko, (Ed.), *Plants in monsoon climate*. Proceedings of the conference devoted to the 50-th anniversary of the Botanical Garden-Institute FEB RAS (41-43). Vladivostok: Dalnauka., (In Russian).
- Morozov, V. L. & Belaya, G. A. (1998b). Principles of phytogene pool and coenotic pool protecting of the most important terrestrial ecosystems in the North-East Asia. In: O. V. Khrapko, (Ed.), *Plants in monsoon climate*. Proceedings of the conference devoted to the 50-th anniversary of the Botanical Garden-Institute FEB RAS (268-270). Vladivostok: Dalnauka., (In Russian).
- Morozov, V. L. & Belaya, G. A. (2009). Ecological specificity of the meadow herbs in steppe-like communities of the Primorsky Territory and the Amur River basin. In: A. V. Belikovich, (Ed.), *Plants in the Monsoon Climate*. V. Proceedings of V Conference "*Plants in Monsoon Climate.*," (99-101). Vladivostok: Dalnauka., (In Russian).
- Neshatayeva, V. Yu. (1988). Vegetation of coastal meadows in East Kamchatka (on the example of Kronotsky state reserve). *Herald of Leningrad State University. Ser. 3, Issue 4, 24*, 35-44 (In Russian).
- Neupokoyeva, E. B., Burundukova, O. L. & Probatova, N. S. (1998). Types of photosynthesis, structural and functional properties of sea coastal halophytes in the south of the Russian Far East. In: O. V. Khrapko, (Ed.), *Plants in monsoon climate*. Proceedings of the International conference devoted to the 50-th anniversary of the Botanical Garden-Institute FEB RAS (126-128). Vladivostok: Dalnauka., (In Russian).
- Petukhova, I. P. (2003). Importance of drought resistance of plants in conditions of monsoon climate of the southern Primorye. In: S. B. Gontcharova, (Ed.), *Plants in monsoon climate*. III: Proceedings of III International conference "*Plants in Monsoon Climate.*," (399-402). Vladivostok: BGI FEB RAS. (In Russian).
- Plants in monsoon climate. (1998). *Proceedings of the conference devoted to the 50-th anniversary of the Botanical Garden-Institute FEB RAS*. O. V. Khrapko (Ed.). Vladivostok: Dal'nauka. (In Russian).
- Plants in monsoon climate. (2003). III. Proceedings of III International conference "*Plants in Monsoon Climate*". S. B. Gontcharova (Ed.). Vladivostok: BGI FEB RAS. (In Russian).
- Plants in monsoon climate. (2007). IV. Proceedings of IV International conference "*Plants in Monsoon Climate*". S. B. Gontcharova (Ed.). Vladivostok: BGI FEB RAS. (In Russian).
- Plants in the Monsoon Climate. (2009). V. Proceedings of V Conference "*Plants in Monsoon Climate*". A. V. Belikovich (Ed.). Vladivostok: Dalnauka., (In Russian).

- Plotnikova, L. S. & Trulevich, N. V. (1974). Vegetation in the middle part of Karaguinsky Island west coast . In: P. I. Lapin, (Ed.). *Phyto-geographical regions of the USSR. Prospects of plant introduction* (36-42). Moscow: Nauka. (In Russian).
- Prilutzky, A. N. (2007). Philosophical, conceptual and methodological problems in contemporary phytocoenology. In: S. B. Gontcharova, (Ed.), *Plants in monsoon climate*, 2006. IV. Proceedings of IV International conference "*Plants in Monsoon Climate*" (6-11). Vladivostok: BGI FEB RAS. (In Russian).
- Probatova, N. S. & Barkalov, V. Yu. (2003). The Grass Family (*Poaceae*) on Sakhalin and the Kuril Islands: a comparative study of taxonomy and distribution. In: *Phytogeography of Northeast Asia: tasks for the 21-st century*. Abstr. of the Symposium (73). Vladivostok.
- Probatova, N. S. & Buch, T. G. (1981). *Hydrilla verticillata* (L. fil.) Royle (Hydrocharitaceae) in the Soviet Far East. *Bot. Journ.*, (Leningrad), 66, 2, 208-214. (In Russian).
- Probatova, N. S. & Rudyka, E. G. (2000). Caryological study on the flora of Russky Island in Peter the Great Bay (the Primorsky Territory). In: O. V. Khrapko, (Ed.), *Monsoon Climate Plants, 2000*. II Intern. conference "*Monsoon Climate Plants*". (Abstr.). (165-166). Vladivostok: Dalnauka., (In Russian).
- Probatova, N. S. & Rudyka, E. G. (2003). Chromosome numbers in vascular flora of the Russian Far East: contemporary stage of the study. In: *Botanical studies in Asiatic Russia, 1*. Proceedings of XI Meeting of the Russian botanical society (311-312). Barnaul: AzBuka Publishing House. (In Russian).
- Probatova, N. S. & Seledets, V. P. (1980). *Rudbeckia hirta* (Asteraceae) on Reineke Island (the Primorsky Territory). *Bot. Journ.*, (Leningrad), 65, 7, 977-982. (In Russian).
- Probatova, N. S. & Seledets, V. P. (1983). Herbaceous plant communities on Bol'shoi Pelis Island as resources for landscape designing. In: *Landscape designing* (Some problems of theory and methods). Vladivostok: 56-63. (In Russian).
- Probatova, N. S. & Seledets, V. P. (1996). Caryological aspect in monitoring of the flora of aquatic and riverside plant communities in the Russian Far East. Abstr. of the Republican conference "*Regional nature management and ecological monitoring*" (276-277). Barnaul: Publishing House of the Altai State University. (In Russian).
- Probatova, N. S. & Seledets, V. P. (1998). Vascular plants in the contact land-ocean zone: the problems of coastal botany in the Russian Far East. In: O.V. Khrapko, (Ed.), *Plants in monsoon climate*. Proceedings of the International conference devoted to the 50-th anniversary of the Botanical Garden-Institute FEB RAS (51-54). Vladivostok: Dalnauka., (In Russian).
- Probatova, N. S. & Seledets, V. P. (1999). Vascular plants in the contact "land-ocean" zone. *Herald of the Far East Branch of the Russian Academy of Sciences* (Vladivostok), 3, 80-92. (In Russian).
- Probatova, N. S. & Shatokhina, A. V. (2007). Chromosome studies on the Grass Family (*Poaceae*) in the Amur River basin. In: *Ecosystem evolution of Baikalian region and adjacent areas in context of global change: past, present, future*. Abstr. of International Symposium (71-73). Irkutsk: The Irkutsk State University Publishing House.
- Probatova, N. S. & Sokolovskaya, A. P. (1981a). Caryological study on vascular plants from the islands of the Far East state marine reserve. In: Yu. D. Chugunov, (Ed.), *Flowering plants of the islands of the Far East marine reserve* (92-114). Vladivostok: Far East Scientific Center of the USSR Academy of Sciences. (In Russian).

- Probatova, N. S. & Sokolovskaya, A. P. (1981b). Chromosome numbers of some species of the Priamurye aquatic and riverside flora, with special reference to peculiarities of its formation. *Bot. Journ.*, (Leningrad), 66, 11, 1584-1594. (In Russian).
- Probatova, N. S. & Sokolovskaya, A. P. (1983). New chromosome number data for vascular plants from the islands of Peter the Great Bay (the Primorsky Territory). *Bot. Journ.*, (Leningrad), 68, 12, 1655-1662. (In Russian).
- Probatova, N. S. & Sokolovskaya, A. P. (1984). Chromosome numbers in representatives of the families Alismataceae, Hydrocharitaceae, Hypericaceae, Juncaginaceae, Poaceae, Potamogetonaceae, Ruppiaceae, Sparganiaceae, Zannichelliaceae, Zosteraceae from the Far East of the USSR. *Bot. Journ.*, (Leningrad), 69, 12, 1700-1702. (In Russian).
- Probatova, N. S. & Sokolovskaya, A. P. (1989). Chromosome numbers in vascular plants from Primorye, Priamurye, Sakhalin, Kamchatka and the Kurile Islands. *Bot. Journ.*, (Leningrad), 74, 1, 120-123. (In Russian).
- Probatova, N. S. (1970). *Glyceria depauperata* Ohwi - new species in the flora of the USSR. *Bot. Journ.* (Leningrad), 55, 6, 876-877. (In Russian).
- Probatova, N. S. (1973). New and rare species of Poaceae from the Far East. *Novitates systematicae plantarum vascularium*, 10, 68-79. Leningrad: Nauka. (In Russian).
- Probatova, N. S. (1974b). On the new genus *Arctopoa* (Griseb.) Probat. (Poaceae). *Novitates systematicae plantarum vascularium*, 11, 44-54. Leningrad: Nauka. (In Russian).
- Probatova, N. S. (1974a). *Gramineae*. In: A. I. Tolmachev, (Ed.), Key for the vascular plants of Sakhalin and Kurile Islands (56-89). Leningrad: Nauka. (In Russian).
- Probatova, N. S. (1981). Family Poaceae (Gramineae). In: S. S. Kharkevich & S. K. Cherepanov (Eds.), *Manual of the vascular plants of Kamchatskaya Oblast.* (332-370). Moscow: Nauka. (In Russian).
- Probatova, N. S. (1984). New taxa of Poaceae from the Far East of the USSR. *Bot. Journ.*, (Leningrad), 69, 2, 251-259. (In Russian).
- Probatova, N. S. (1985). *Poaceae* Barnh. In: S. S. Kharkevich, & N. N. Tzvelev (Eds.), *Vascular plants of the soviet Far East*, 1 (89-382). Leningrad: Nauka. (In Russian).
- Probatova, N. S. (1995a). The genus *Arctopoa* (Griseb.) Probat. (*Poaceae*): Siberian - North Pacific contacts. In: *Problems in studies of the Siberian plant cover*. Abstr. of the conference (51-53). Tomsk: Tomsk University Press (In Russian).
- Probatova, N. S. (1995b). *The North Pacific area: a zone of speciation for Poaceae*. In: XVIII Pacific Science Congress. Abstr. (192). Beijing, China.
- Probatova, N. S. (1997a). *On the problem of the grass flora genesis in the N Pacific islands: the Commander Islands*. In: P. Ya. Baklanov & L. D. Filatova (Eds.), *Geographical studies in the Far East*. Proceedings of the conference devoted to the 150-th anniversary of the Russian geographical society (149-151). Vladivostok: Dalnauka., (In Russian).
- Probatova, N. S. (1997b). *Taxonomic problems in biodiversity of the thick-rhizomatous sweet-grasses (*Hierochloë* R. Br., *Poaceae*) in the North-East Asia* Probatova, N. S. (1998). Caryology of the vascular flora in the south of the Russian Far East: analytical aspect. In: O.V. Khrapko, (Ed.), *Plants in monsoon climate*. 1998. Proceedings of the Conference devoted to the 50-th anniversary of the Botanical Garden-Institute FEB RAS (132-134). Vladivostok: Dalnauka., (In Russian).
- Probatova, N. S. (2000). Caryology and the nature protection problems of the bank flora in the temperate regions of the monsoon climate. In: O. V. Khrapko, (Ed.), *Monsoon*

- Climate Plants. 2000. II International conference "*Monsoon Climate Plants*". (Abstr.). (163-164). Vladivostok: Dalnauka., (In Russian).
- Probatova, N. S. (2003a). Family *Poaceae*. In: S. S. Kharkevich, & N. N. Tzvelev (Eds.), *Vascular Plants of the Russian Far East. Vol. 1. Lycopodiophyta, Juncaceae, Poaceae (Gramineae)* (87-488). Science Publishers Inc., Enfield, New Hampshire, USA.
- Probatova, N. S. (2003b). The genus *Arctopoa* (Griseb.) Probat. (Poaceae) taxonomy, chromosome numbers, biogeography, differentiation. *Komarov Memorial Lectures* (Vladivostok), 49, 89-130. (In Russian).
- Probatova, N. S. (2003c). Chromosome numbers of plant species as a source of information in studies on the flora of the Russian Far East. *Herald of the Far East Branch of the Russian Academy of Sciences* (Vladivostok), 3, 54-67. (In Russian).
- Probatova, N. S. (2004). Specific features of the Russian Far East representatives of the Family Poaceae, in comparison with Siberia. In: *Problems of conservation of the Inner Asia vegetation, I*. Proceedings of the scientific conference (169-171). Ulan-Ude: Buryat Scientific Center SB RAS Publishers. (In Russian).
- Probatova, N. S. (2006). Poaceae. In: A. E. Kozhevnikov, & N. S. Probatova (Eds.), *Flora of the Russian Far East. Addenda and corrigenda to "Vascular plants of the Soviet Far East", vols. 1-8 (1985-1996)* (327-391). Vladivostok: Dalnauka., (In Russian).
- Probatova, N. S. (2007). Chromosome numbers in the Family Poaceae and their significance for systematics, phylogeny, and phytogeography (the Russian Far East). *Komarov Memorial Lectures* (Vladivostok), 55, 9-103. (In Russian).
- Probatova, N. S. (2008). Caryological study of Poaceae in the contact land-ocean zone (Russian Far East). In: M. E. Ermokhin, (Ed.), *Problems of marginal structures of biocoenoses*. Proceedings of the 2-d All-Russia scientific conference with international participation (206-210). Saratov: Saratov State University Press. (In Russian).
- Probatova, N. S., Barkalov, V. Yu. & Rudyka, E. G. (2004). Chromosome numbers of selected vascular plant species from Sakhalin, Moneron and the Kurile Islands. In: H. Takahashi & M. Ōhara (Eds.), *Biodiversity and Biogeography of the Kuril Islands and Sakhalin, 1*. (Bulletin of the Hokkaido University Museum, 2) (15-23). Hokkaido University Museum, Sapporo, Japan.
- Probatova, N. S., Barkalov, V. Yu. & Rudyka, E. G. (2007). Caryology of the flora of Sakhalin and the Kurile Islands. *Chromosome numbers, taxonomic and phytogeographical comments*. Vladivostok: Dalnauka., (In Russian, with English parts).
- Probatova, N. S., Barkalov, V. Yu., Rudyka, E. G. & Kozhevnikova, Z. V. (2009). Additions to chromosome numbers for vascular plants from Sakhalin and the Kurile Islands (1). In: H. Takahashi & M. Ōhara (Eds.), *Biodiversity and Biogeography of the Kuril Islands and Sakhalin, 3*. (Bulletin of the Hokkaido University Museum, n° 5) (35-47). Sapporo: Hokkaido University Museum (Japan).
- Probatova, N. S., Barkalov, V. Yu., Rudyka, E. G. & Pavlova, N. S. (2006). Further chromosome studies on vascular plant species from Sakhalin, Moneron and Kurile Islands. In: H. Takahashi, & M. Ōhara, (Eds.), *Biodiversity and Biogeography of the Kuril Islands and Sakhalin, 2*. (Bulletin of the Hokkaido University Museum, n° 3) (93-110). Sapporo: Hokkaido University Museum (Japan).
- Probatova, N. S., Barkalov, V. Yu., Rudyka, E. G. & Shatalova, S. A. (2000). Chromosome study on vascular plants of the Kurile islands. In: T. Komai, (Ed.), *Results of recent*

- research on Northeast Asian biota. *Nat. Hist. Res., Special Issue*, 7 (21-38). Chiba: Natural History Museum and Institute (Japan).
- Probatova, N. S., Bezdeleva, T. A. & Rudyka, E. G. (2001). Chromosome numbers, taxonomy and geographical distribution of the Far Eastern *Viola* (Violaceae). *Komarov Memorial Lectures* (Vladivostok), 48, 85-124. (In Russian).
- Probatova, N. S., Kozhevnikova, Z. V., Rudyka, E. G., Kozhevnikov, A. E. & Nechaev V. A. (2010). Chromosome numbers of some vascular plants from the Far East of Russia. *Bot. Journ.*, (Leningrad), 95, 7, 1008-1020. (In Russian).
- Probatova, N. S., Rudyka, E. G. & Barkalov, V. Yu. (2003). Caryological studies on the vascular flora of sea coasts and islands of the Russian Far East. In: S. B. Gontcharova, (Ed.), *Plants in monsoon climate*, 2003, III. Proceedings of III International conference "Plants in monsoon climate" (283-288). Vladivostok: BGI FEB RAS. (In Russian).
- Probatova, N. S., Rudyka, E. G. & Shatokhina, A. V. (2007). Advance in chromosome numbers study on vascular flora of the Russian Far East in 2000-2006. In: S. B. Gontcharova, (Ed.), *Plants in monsoon climate*, 2006, IV. Proceedings of IV International conference "Plants in Monsoon Climate" (11-29). Vladivostok: BGI FEB RAS. (In Russian).
- Probatova, N. S., Rudyka, E. G. & Sokolovskaya, A. P. (1998). Chromosome numbers in vascular plants from the islands of Peter the Great Bay and Muravyev-Amursky Peninsula (the Primorskii Territory). *Bot. Journ.*, (St.-Petersbourg), 83, 5, 125-130. (In Russian).
- Probatova, N. S., Rudyka, E. G., Kozhevnikov, A. E. & Kozhevnikova, Z. V. (2004). Chromosome numbers in representatives of the flora of the Primorsky Territory. *Bot. Journ.*, (St. Petersburg), 89, 7, 1208-1216. (In Russian).
- Probatova, N. S., Seledets, V. P. & Barkalov, V. Yu. (2003). Vascular plants in the contact "land-ocean" zone [the Russian Far East]. First approach // *Phytogeography of Northeast Asia: tasks for the 21-st century*. Abstr. of the Symposium (74). Vladivostok.
- Probatova, N. S., Seledets, V. P. & Sokolovskaya, A. P. (1984). Sea coastal halophilous plants of the soviet Far East: chromosome numbers and ecology. *Komarov Memorial Lectures* (Vladivostok), 31, 89-116. (In Russian).
- Probatova, N. S., Seledets, V. P., Barkalov, V. Yu. & Rudyka, E. G. (2005). Principal results and aspects of the studies on vascular plant biodiversity in the contact land-ocean zone (the Russian Far East). In: O. V. Khrapko (Ed.). *Rhythms and catastrophes impact on the vegetation of the Russian Far East*. Proceedings of the International conference (112-121). Vladivostok: BGI FEB RAS. (In Russian).
- Probatova, N. S., Seledets, V. P., Nedoluzhko, V. A. & Pavlova, N. S. (1998). *Vascular plants in the islands of Peter the Great Bay, Sea of Japan* (the Primorsky Territory). Vladivostok: Dalnauka., (In Russian).
- Probatova, N. S., Sokolovskaya, A. P. & Rudyka, E. G. (1989). Chromosome numbers in some species of vascular plants from Kunashir Isl., the Kurile Islands. *Bot. Journ.*, (Leningrad), 74, 11, 1675-1678. (In Russian).
- Probatova, N. S., Sokolovskaya, A. P. & Rudyka, E. G. (1996). Chromosome numbers in species of *Hierochloë* (*Poaceae*) on the Far East of Russia. *Bot. Journ.*, (St.-Petersbourg), 81, 4, 119-121. (In Russian).

- Probatova, N.S. & Seledets, V.P. (1997). Problems in coastal plant biodiversity studies and conservation on the Russian Far East. In: V. L. Kassyanov, (Ed.), *Global change studies at the Far East*. Abstr. of Workshop (29-30). Vladivostok: Dalnauka.,
- Pshenichnikov, B. F. (2003). Individuality of the islands burozems formation and evolution under condition of the monsoon climate of the southern part of the Far East. In: S. B. Gontcharova, (Ed.), *Plants in monsoon climate*, 2003, III. Proceedings of III International conference "Plants in Monsoon Climate" (124-129). Vladivostok: BGI FEB RAS (In Russian).
- Ramensky, L. G. & Tsatsenkin, I. A. (1968). *Ecological evaluation of the forage grasslands in the Caucasus, by vegetation cover*. Moscow: Publishing House of the V. R. Williams All-Union Forage Institute. (In Russian).
- Ramensky, L. G. (1910). On comparative method of ecological study of plant communities. In: *Diary of XII Congress of Russian naturalists and physicians*, 7, 389-390. St.-Petersbourg. (In Russian).
- Ramensky, L. G. (1938). *Introduction into complex soil-geobotanical study of lands*. Moscow: Selkhozgiz. (In Russian).
- Ramensky, L. G. (1971). *Selected Works. Problems and methods of vegetation study*. Leningrad: Nauka. (In Russian).
- Ramensky, L. G., Tsatsenkin, I. A., Chizhikov, O. N. & Antipin, N. A. (1956). *Ecological estimation of grasslands on the base of the vegetation cover study*. Moscow: Selkhozgiz. (In Russian).
- Rothera, S. L. & Davy, A. J. (1986). Polyploidy and habitat differentiation in *Deschampsia cespitosa*. *New Phytol.* 102, 449-467.
- Safronova, I. N. & Yurkovskaya, T. K. (2007). Vegetation cover of Pacific Northern Eurasia on geobotanical map scale 1: 15,000,000 for the National Atlas of Russia. In: S. B. Gontcharova, (Ed.), *Plants in monsoon climate*, 2006, IV. Proceedings of IV International conference "Plants in Monsoon Climate" (3-5). Vladivostok: BGI FEB RAS. (In Russian).
- Schlothgauer, S. D. (2009). Zoning development of ecosystems regeneration capacities on the example of the Russian Far East central part. In: A. V. Belikovich, (Ed.), *Plants in the Monsoon Climate*, 2009, V. Proceedings of V Conference "Plants in Monsoon Climate" (215-218). Vladivostok: Dalnauka.,
- Seledets, V. P. & Probatova, N. S. (1981). Supplement to the flora of the islands of the Far East state marine reserve. In: Yu. D. Chugunov, (Ed.), *Flowering plants of the islands of the Far East marine reserve* (81-91). Vladivostok: Far East Scientific Center of the USSR Academy of Sciences. (In Russian).
- Seledets, V. P. & Probatova, N. S. (1989). Polyploidy and ecological-coenotic relationships in plants (on the example of the Soviet Far East flora). In: *2-d Conference on plant caryology*. Abstr. of papers (23-25). Novossibirsk: Central Siberian Botanical Garden, Siberian Division of the USSR Academy of Sciences. (In Russian).
- Seledets, V. P. & Probatova, N. S. (2003a). Ecological scales as a source of information on ecology of plant diversity (Poaceae of the Russian Far East). *Komarov Memorial Lectures* (Vladivostok), 49, 89-130. (In Russian).
- Seledets, V. P. & Probatova, N. S. (2003b). Ecological range and some problems of differentiation in the Grass Family (Poaceae) of the Russian Far East. In: A. P. Kryukov & L. V. Yakimenko (Eds.), *Problems of Evolution*, 5 (213-220). Vladivostok: Dalnauka.,

- Seledets, V. P. & Probatova, N. S. (2007a). Ecological ranges of plant species: essay of study. In: S. B. Gontcharova, (Ed.), *Plants in monsoon climate*, 2006. IV: Proceedings of IV International conference "Plants in Monsoon Climate" (85-88). Vladivostok: BGI FEB RAS. (In Russian).
- Seledets, V. P. & Probatova, N. S. (2007b). *Ecological range of plant species*. Vladivostok: Dalnauka., (In Russian).
- Seledets, V. P. (1969). Phytogeographical regionalization of Iturup Island (South Kuriles). In: L. N. Vassilyeva, (Ed.), *Problems in botany in the Far East*. The Centenary of Academician V. L. Komarov (1869-1969) (181-192). Vladivostok: Far East Branch of Siberian Division of the USSR Academy of Sciences. (In Russian).
- Seledets, V. P. (1970). On ecology and phytocoenology of coastal zone vegetation in Iturup Island. Proceedings of the Siberian Branch of the USSR Academy of Sciences, *Biol.*, 5, 9-14. (In Russian).
- Seledets, V. P. (1975). *Application of ecological scales for study of anthropogenic dynamics of vegetation in suburban areas of the Far East*. In: XII International Botanical Congress. Abstr. of papers, 2 (553). Leningrad. (In Russian).
- Seledets, V. P. (1976b). Ecology of sea coastal grasses (*Poaceae*) in the Far East. *Ecology*, 2, 19-23. (In Russian).
- Seledets, V. P. (1976a). Application of the ecological scales method in botanical studies in the soviet Far East. *Komarov Memorial Lectures* (Vladivostok), 24, 62-78. (In Russian).
- Seledets, V. P. (1977). Ecology of the sea coastal plant communities in the Far East. In: *Wild flora of the Far East* (18-33). Vladivostok: Far East Scientific Center of the USSR Academy of Sciences. (In Russian).
- Seledets, V. P. (1978a). Sea coastal vegetation dynamics in the south of the soviet Far East. In: S. S. Kharkevich, (Ed.), *Botanical studies in the Far East*. Transactions of the Institute of Biology & Soil Science, new ser., 51 (154) (110-115). Vladivostok: Far East Scientific Center of the USSR Academy of Sciences. (In Russian).
- Seledets, V. P. (1978b). Anthropogenic dynamics of the herb layer of oak forests in Vladivostok forest park. In: *Contemporary problems of nature protection on the Far East* (38-43). Vladivostok: Far East Scientific Center of the USSR Academy of Sciences. (In Russian).
- Seledets, V. P. (1980). Ecological tables for herbaceous plants of Primorye and Priamurye, for phytomelioration. In: *Rational use and protection of land resources of the Far East* (160-170). Vladivostok: Far East Scientific Center of the USSR Academy of Sciences. (In Russian).
- Seledets, V. P. (1981). Vegetation of the Bol'shoi Pelis Island. In: Yu. D. Chugunov, (Ed.), *Flowering plants of the islands of the Far East marine reserve* (115-129). Vladivostok: Far East Scientific Center of the USSR Academy of Sciences. (In Russian).
- Seledets, V. P. (1982). Application of ecological scales for study of hayfields and pastures of the soviet Far East and measures for their improving. In: S. S. Kharkevich, (Ed.), *Wild forage grasses of the soviet Far East* (202-229). Moscow: Nauka. (In Russian).
- Seledets, V. P. (1985). Ecological and geographical classification of habitats of rare vascular plant species of the soviet Far East. In: *Protection of rare species of vascular plants at the Soviet Far East* (181-195). Vladivostok: Far East Scientific Center of the USSR Academy of Sciences. (In Russian).



- Seledets, V. P. (1988). Plant communities on the seacoasts of the Far East. In: L.V. Sozinov & B. I. Semkin (Eds.), *Structural organization of ecosystems components* (comparative and quantitative analysis) (35-46). Vladivostok: Far East Branch of the USSR Academy of Sciences. (In Russian).
- Seledets, V. P. (2000b). *Plant cover of the nature monuments in the islands of Peter the Great Bay* (the Primorsky Territory). North Pacific islands biological research (Vladivostok), 4, 1-72 (In Russian).
- Seledets, V. P. (2000c). Ecological evaluation of habitats and protection of the plant cover in the Far East of Russia. In: O.V. Khrapko, (Ed.), *Monsoon Climate Plants*, 2000. II International conference "Monsoon Climate Plants". (Abstr.), (187-188). Vladivostok: Dalnauka., (In Russian).
- Seledets, V. P. (2000d). Experience of application of the ecological scales method to the study of plant cover in monsoon climate of the Russian Far East. In: *Problems in study of the plant cover of Siberia*. 2-d Russian scientific conference devoted to the 150th anniversary of P. N. Krylov (130-131). Abstr. Tomsk: Tomsk University Press. (In Russian).
- Seledets, V. P. (2000a). *Ecological scales for vegetation studies in the Russian Far East*. Vladivostok: Publishing House of the Far East Academy of Economics and Management. (In Russian).
- Seledets, V. P. (2001). Characteristics and structure of ecological areas of vascular plant species of the Far East, in connection with the problem of biodiversity conservation. In: V. P. Seledets, (Ed.), *V-th Far-Eastern Conference on nature conservation problems*, devoted to 80-th anniversary of Academician A. V. Zhirmunsky (250-251). Vladivostok: Dalnauka., (In Russian).
- Seledets, V. P. (2003a). Ecological differentiation of coastal coenopopulations in the Russian Far East. In: S. B. Gontcharova, (Ed.), *Plants in monsoon climate*, 2003, III. Proceedings of III International conference "Plants in Monsoon Climate" (292-295). Vladivostok: BGI FEB RAS. (In Russian).
- Seledets, V. P. (2003b). Ecological ranges of coenotic populations in different parts of the species areas of distribution. In: *Phytogeography of Northeast Asia: tasks for the 21st century*. Abstr. of the Symposium (p. 86). Vladivostok.
- Seledets, V. P. (2004). Ecological ranges of species in coastal and continental areas. In: Problems of conservation of the Inner Asia vegetation, I. Proceedings of the scientific conference (10-11). Ulan-Ude: Buryat Scientific Center SB RAS Publishers. (In Russian).
- Seledets, V. P. (2006). Ecological ranges of plant species at the Russian Pacific coast in comparison with intracontinental regions. *Komarov Memorial Lectures* (Vladivostok), 53, 54-100. (In Russian).
- Seledets, V. P. (2009a). Comparative ecological study of continental and insular coenopopulations of *Leymus mollis* (Poaceae) in the Russian Far East. *Bot. Journ.*, (St.-Petersbourg), 94, 3, 397-405. (In Russian).
- Seledets, V. P. (2009b). Ecological ranges of plant species and their transformation in the contact land-ocean zone (Russian Far East). In: *Ecology of biosystems: the problems of study, indication and forecasting*. Proceedings of II International scientific and practical conference (273-277). Astrakhan: Astrakhan State University Press. (In Russian).

- Seledets, V. P. (2009c). Ecological ranges of the plant species in the continental and ocean regions of Asian Russia. *Sib. Ecol. Journ.* 16, 4, 529-538. (In Russian); *Contemporary Problems of Ecology*, 2, 4, 314-320.
- Seledets, V. P. (2010a). Ecological ranges of invasive grass species (Poaceae) in the Russian Far East. *Bot. Journ.*, (St. Petersburg), 95, 4, 548-562. (In Russian).
- Seledets, V. P. (2010b). Comparative analysis of ecological ranges of *Agrostis tririi* and *Calamagrostis brachytricha* (Poaceae) on the east limit of the species geographical distribution (Russian Far East). *Bot. Journ.*, (St. Petersburg), 95, 9, 1308-1321 (in press) (In Russian).
- Sobolev, L. I. (1971). Delimitation of elementary typological units of plant cover by L. G. Ramensky method. In: *Methods of delimitation of plant associations* (105-110). Leningrad: Nauka. (In Russian).
- Sobolev, L. I. (1975). Ecology and typology of the lands. *Ecology*, 4, 20-29. (In Russian).
- Sobolev, L. I. (1978). *Method of ecological and typological studies of lands*. Frunze: Ilim. (In Russian).
- Sokolovskaya, A. P. & Probatova N. S. (1973b). Chromosome numbers in the Far East species of *Glyceria* R. Br. *Bot. Journ.*, (Leningrad), 58, 9, 1342-1347. (In Russian).
- Sokolovskaya, A. P. & Probatova, N. S. (1968). Caryotaxonomic study on the Far East species of *Poa* L. *Bot. Journ.*, (Leningrad), 53, 12, 1737-1743. (In Russian).
- Sokolovskaya, A. P. & Probatova, N. S. (1973a). Caryotaxonomic study on the Far East species of *Poa* L., II. *Bot. Journ.*, (Leningrad), 58, 1, 89-96. (In Russian).
- Sokolovskaya, A. P. & Probatova, N. S. (1974). Caryotaxonomic study on the Far East species of *Agrostis* L. *Bot. Journ.*, (Leningrad), 59, 9, 1278-1287. (In Russian).
- Stebbins, G. L. (1984). Polyploidy and the distribution of the arctic-alpine flora: new evidence and a new approach. *Bot. Helv.* 94, 1-13.
- Stepanova, K. D. (1985). Meadows of Kamchatskaya oblast. Vladivostok: Far East Scientific Center of the USSR Academy of Sciences. (In Russian).
- Takahashi, H. (2009). Geographical distribution patterns of the Apiaceae in Sakhalin and the Kuril Islands. In: H. Takahashi & M. Ōhara (Eds.), *Biodiversity and Biogeography of the Kuril Islands and Sakhalin*, 3. (Bulletin of the Hokkaido University Museum, 5) (1-34). Hokkaido University Museum, Sapporo, Japan.
- Tateoka, T. (1973). A taxonomic study of the *Poa macrocalyx* complex, with particular reference to the population in Eastern Hokkaido. *Bot. Mag. Tokyo*, 86, 1003, 213-228.
- Tsatsenkin, I. A. & Kassach, A. I. (1970). *Ecological evaluation of grasslands and pastures in Pamirs by vegetation cover*. Dushanbe: Donish. (In Russian).
- Tsatsenkin, I. A. (1967). *Ecological scales for grasslands and pastures in mountain and plain regions of Central Asia, Altai and Urals*. Dushanbe: Donish. (In Russian).
- Tsatsenkin, I. A. (1970). *Ecological evaluation of the forage grasslands in Carpatian and Balkan Mts. by vegetation cover*. Moscow: V.R. Williams All-Union Research Forage Institute. (In Russian).
- Tsatsenkin, I. A., Dmitrieva, S. I., Belyaeva, N. V. & Savchenko, I. V. (1974). *Methodical guideline for ecological evaluation of the forage grasslands in steppe and steppe-forest zones of Siberia by vegetation cover*. Moscow: V. R. Williams All-Union Research Forage Institute. (In Russian).
- Tsatsenkin, I. A., Savchenko, I. V. & Dmitrieva, S. I. (1978). *Methodical guideline for ecological evaluation of the forage grasslands in tundra and forest zones of Siberia and*

- the Far East by vegetation cover*. Moscow: V. R. Williams All-Union Research Forage Institute. (In Russian).
- Tsyganov, D. N. (1974). Ecomorphes and ecological suites. *Bull. Moscow Society of Naturalists*, *Biol.* 79, 2, 128-141. (In Russian).
- Tzvelyov, N. N. & Probatova, N. S. (2010). New taxa of Poaceae from Russia. *Bot. Zhurn.*, (St.-Petersbourg), 95, 6, 857-869. (In Russian).
- Vascular plants of the Soviet Far East*. (1985-1996). S. S. Kharkevich (Ed.). Vol. 1, 1985; vol. 2, 1987; vol. 3, 1988; vol. 4, 1989; vol. 5, 1991; vol. 6, 1992; vol. 7, 1995; vol. 8, 1996. Leningrad-St.-Petersbourg: Nauka. (In Russian).