

Ecological Ranges and Types of Rarity in the Kuznetsk Alatau of Some *Saussurea* DC. Species

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Abstract—An analysis of indicator values of four *Saussurea* DC. species, *S. baicalensis* (Adams) B. L. Rob., *S. frolowii* Ledeb., *S. salicifolia* (L.) DC., and *S. schanginiana* (Wydl.) Fisch. ex Serg., have been carried out by the method of indicator scales of soil moisture and nutrient availability and salinity in more than 1600 relevés. The size of their ecological ranges and the values of their competitiveness in phytocenoses are determined. As a result of a comparison of the locality of local populations within the ecological range and their occurrence, the vulnerability of *S. baicalensis*, *S. frolowii*, *S. salicifolia*, and *S. schanginiana* in the Kuznetsk Alatau is evaluated. The types of rarity for these species in the Kuznetsk Alatau are determined.

Keywords: ecological niche, analysis of species indicator values, *Saussurea*, the Kuznetsk Alatau, rarity

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INTRODUCTION

No universally accepted definition of “rare species” in the botanical literature exists (Zlobin et al., 2013). The definition of K.D. Gaston (1994, p. 11) is widely cited: “~~rare species are species with a small number and/or a small habitat~~.” According to him, rarity is a complex concept that involves a comparison between populations or species. He accented the rarity relativity and proposed to apply the epithet “rare” to 25% species of the least abundant in a plant community and to 25% of the species with the ~~lowest species distribution area~~. This proposal allows significant simplification, which could result in the risk of attributing the majority of species in the study area to rare species (Holt, 1997). To narrow down and specify the concept of “rare species,” botanists have been developing criteria for rarity; confinement to a specific habitat (habitat specificity) was recognized as one of the characteristics of vulnerable species in need of protection (Given, Williams, 1984; Faber-Langendoen et al., 2012). A widely used rarity model was proposed by D. Rabinowitz (1981), which classifies species based on three criteria: geographical ~~distribution~~ (wide or narrow), habitat specificity (small or large), and abundance ~~of~~ community (high or low). According to the key on these simple but objective criteria, only one of the eight possible combinations can be classified as “normal,” i.e., an abundant species dedicated to nonspecific habitats with a wide geographic range. The other seven combinations correspond to one of the types of rarity. J. Rey Benayas et al. (1999) later developed Rabinowitz’s model, adding a fourth

criteria in order to divide rare and common species of plants: habitat occupancy.

Since the habitat specificity is low tolerance to environmental conditions (Lindenmayer, Burgman, 2006), it is valid to judge it only after studying the ecology of the taxon. The doctrine of the environmental personality of the species was independently formulated by L. Ramenskii (1910) and H. A. Gleason (1917, 1924). Subsequently, on the basis of this doctrine, the ecological scales methodology was developed (Ramenskii 1938, 1971; Ellenberg, 1950), and lists of species indicator values that define the plants’ status on the gradient of some environmental factors were published (Ramenskii et al., 1956; Tsatsenkin, 1967; Tsatsenkin et al., 1974, 1978; Landolt, 1977; Tsyganov, 1983; Hundt, 1966; Ellenberg, 1974; Frank, Klotz, 1990; Ellenberg et al., 1992.; Korolyuk, 2006; Troeva et al., 2010; Landolt et al., 2010 and others). Most of these tables include environmental information on differentiating the most important factors for vegetation: ~~moisturizing~~ and nutrient availability and salinity (Bulohov, 2004; Zverev, 2007, 2009). For a description of the environmental conditions required to maintain viable populations, the concept of “ecological niche” was developed (Hutchinson, 1957; Begon et al., 2006). According to this concept, ecological niche dimensionality depends on the number of investigated conditions—factors. As a cornerstone of theoretical ecology (Alley, 1982; Devictor et al., 2010.; Pocheville, 2015), this concept is widely used by ecologists and botanists during predictive mapping of plant populations (Irfan-Ullah et al., 2007; Solano,

Feria, 2007), microevolutionary processes studies (Friberg et al., 2008), studies of dispersal pathways of invasive species (Albright et al., 2010; Thuiller et al., 2012), searching for the best areas for growing crops (Sanchez et al., 2010), and reintroduction (Griscom, Griscom, 2012). The analysis of species indicator values by the method of ecological scales is one of the most widely used and effective methods for the study of ecological niche (Diekmann, 2002; Zhukova, 2004; Nekratova, Nekratov, 2005; Zubkova, 2009; Zhukova et al., 2010; Komarov, Zubkova, 2012). In 2007, V.P. Seledets and N.S. Probatova offered the concept of “ecological range,” which refers to the distribution of species cenopopulation in an expanse of environmental factors, which illustrates the internal ecological diversity of a species as a basic taxonomic unit. Ecological range is an indicator of plasticity of a species and its ability to inhabit a variety of environmental conditions. It allows one to evaluate in conventional units the adaptive potential of species, that is, its stenotopic and eurytopic (habitat versatility). It is obvious that the concepts of “ecological niche” and “ecological range” are similar, so we believe that they can be used as synonyms. The approach to the analysis of the ecological ranges (niches) with the use of ecological scales was developed in detail (Seledets, Probatova, 2007; Seledets, 2009, 2010), which made it convenient to study rare species. The probability that changes of habitat abiotic conditions may soon result in a reduction of the range of a rare plant depends, firstly, on the size of the environmental range: stenotopic types in this case are the most vulnerable. Second, the vulnerability of the local populations of the species can be evaluated by their location inside the ecological range: sensitivity to environmental factors changes usually demonstrates a population that grows on the border of the ecological niche.

We used this approach to evaluate the vulnerability of four rare species of *Saussurea* DC. in the Kuznetsk Alatau: *S. baicalensis* (Adams) B.L. Rob., *S. frolowii* Ledeb., *S. salicifolia* (L.) DC., and *S. schanginiana* (Wydl.) Fisch. ex Serg. *S. frolowii* was registered in the Kuznetsk Alatau in 22 localities, *S. baicalensis* and *S. schanginiana* in 5, and *S. salicifolia* in 4 localities (Shurupova, 2015). A large number of locations and conflicting information about the status of *S. frolowii* populations gave occasion to exclude this species from the list of plants needing protection in Kemerovo oblast (Red Book..., 2000, 2012). At the present time, none of *Saussurea* species is included in the Red Book of the Republic of Khakassia (2002) and Kemerovo oblast (2012).

The aim of our study was to determine the value of ecological ranges of four *Saussurea* species growing in the Kuznetsk Alatau; to evaluate their vulnerability and determine rarity types.

MATERIALS AND METHODS

An analysis of species indicator values was performed using a gradient module of integrated botanical information system IBIS (Zverev, 2007, 2012) on 1620 relevés data. In this data set, *S. baicalensis* (11 relevés), *S. frolowii* (281 relevés), *S. salicifolia* (1227 relevés), and *S. schanginiana* (206 relevés) were recorded. Relevés were done by several researchers (including the authors of the article) in different years and cover the areas of Siberia, where the geographic range of the studied *Saussurea* species is partially located. The analysis is based on the method of ecological scales (Ramenskii et al., 1956; Tsyganov, 1983; Korolyuk et al., 2005) and carried out by moisture and nutrient availability and salinity factors using the association of scale reflecting realized optima and amplitudes (Tsatsenkin et al., 1974, 1978), because the relevés were made in the taiga and forest-steppe zones of Siberia. Optimums for taxons represented in both scales were calculated as the arithmetic mean, and tolerance amplitudes were appointed to the highest possible extension of the boundaries. Evaluating species indicator values of each description was done by the method of the weighted average (on the cover of indicator taxons) taking into account their stenotopic (Zverev, Babeshina, 2009). The scale of coverage with 9 points, calculated as a geometric progression members to step 1.930679 (Zverev, 2007), was taken. The interval index of environmental agreement was calculated to assess the degree of homogeneity of habitat conditions on selected factors (Zverev, 2011). This index shows the degree of coherence of environmental preferences of taxons growing together. The average part of indicator species (ratio of the number of taxons with the ecological status of the scale to the total number of the community registered taxons) in the analyzed relevés was $86.1 \pm 0.3\%$ by moisture factor and $85.6 \pm 0.3\%$ by nutrient availability and salinity factor. The average index of the environmental coherence of relevés was $52.8 \pm 0.1\%$ and $59.7 \pm 0.1\%$, respectively. This allows one to trust the received combined scales to considered two factors and settle payments on them.

As an indicator of the studied *Saussurea* species abundance, their projective cover in plant communities were taken; it was analyzed in the same sample set (1620 relevés). The conventional square unit (CSU), a part of the ecological range equal to one level of moisture scale (M) and one level of nutrient availability and salinity scale (NS), was used during ecological range evaluation. Ecological range scale values were used as in Seledets and Probatova classification (2007). Types of *Saussurea* species rarity were set using Rabinowitz' criteria (1981) in the modification of Benayas et al. (1999).

The characteristics of moisture and nutrient availability and salinity of studied *Saussurea* species habitats are given in the table.

Habitat characteristics of four *Saussurea* rare species for the Kuznetsk Alatau of the factors of moisture, and nutrient availability and salinity of soil

Species	<i>N</i>	Moisture		Nutrient availability and salinity of soil	
		Levels (<i>Me/lim</i>)	Scale ranges	Levels (<i>M/lim</i>)	Scale ranges
<i>S. baicalensis</i>	11	64.4/52.2–65.9	Meadow–steppe meadow wet–meadow	8.9/8.1–10.6	mesotrophic rich enough
<i>S. frolowii</i>	280	65.0/62.1–67.1	meadow wet–meadow	9.7/7.9–12.7	mesotrophic rich enough
<i>S. salicifolia</i>	1129	52.8/40.4–67.6	mid-steppe wet–steppe meadow wet–meadow	12.7/9.7–17.1	mesotrophic rich enough rich weak salinity
<i>S. schanginiana</i>	206	62.5/51.5–67.1	wet–steppe meadow wet–meadow	9.8/7.1–12.5	mesotrophic rich enough

N, sample size; *Me*, median; and *lim*, limit of the sample values. Scaled graduation which gets most of the relevés is in bold.

RESULTS AND DISCUSSION

Sampling of relevés with *S. baicalensis* is small, since this species is rare in many Siberia regions (Red Book..., 2000, 2006, 2012). Its cenopopulations dispersed in a limited expansion of environmental factors (Fig. 1). The ecological range of the species is very narrow (“very small” in Seledets and Probatova classification (2007)): its value is 63 CSU. The species is

commonly present in habitats with the moisture regime of lush and wet meadows on poor soils. In the mountainous regions of Siberia such habitats are generally located in the subalpine and alpine zones (Kuminova, 1960; Tanzybaev, 1976). However, the values of the factors of the relevé with *S. baicalensis* from southeastern Transbaikal are very different: this species is recorded here in a habitat with wet–steppe moisture conditions and relatively rich soil.

Besides habitat conditions, the distribution of this species is limited by the high risks associated with the plant propagation process. Unlike *S. frolowii*, *S. salicifolia*, and *S. schanginiana*, which are perennial polycarpic (Shurupova, 2013; Shurupova, Gureeva, 2014; Shurupova et al., 2014a), *S. baicalensis* is long-term monocarpic (Shurupova et al., 2014b; Shurupova, 2015). After seed dispersal at the age of 5–9 years, individuals die.

Three habitats of *S. baicalensis* in two locations in the Kuznetsk Alatau were investigated: Vershina Turgayula (the Republic of Khakassia, Shirinskii district) and Khazyr-Teren mountains (the Republic of Khakassia, Ust'-Abakan district). The moisture and nutrient availability and salinity conditions in the habitat of the mountain Khazyr-Teren, where only 3 *S. baicalensis* individuals were found, were close to the conditions of the depressed cenopopulation habitat on the mountain Vershina Turgayula ($M = 64$ –65; $NS = 8$). Both cenopopulations grow in the alpine tundra and are extremely thin. Therefore, this area of ecological range is located on the border of the possibility of existence of the species. It should be noted that 6 out of 11 relevés with *S. baicalensis* that constituted the sample were located in this part of the ecological range. The second population from the mountain The Vershina Turgayula grows on the upper boundary of the forest zone in

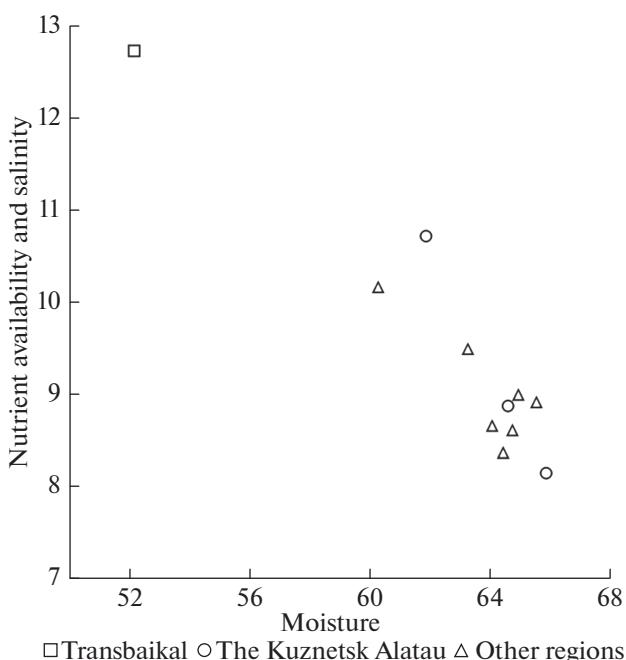


Fig. 1. Distribution of *Saussurea baicalensis* local populations in the extension of factors of moisture and nutrient availability and salinity of soil.

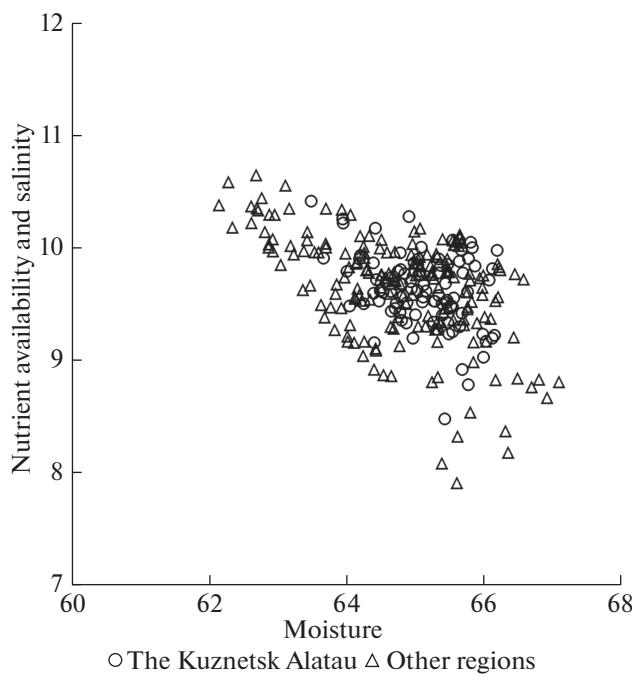


Fig. 2. Distribution of *Saussurea frolowii* local populations in the extension of factors of moisture and nutrient availability and salinity of soil.

the larch (*Larix sibirica* Ledeb) rare forest and located in a less humid ($M = 62$) habitat with richer soils ($NS = 10$). Its ontogenetic and vital structure shows more or less stable conditions (Shurupova, 2015). Mountain zone of the Kuznetsk Alatau is located on the border of the ecological niche of *S. baicalensis*, and the populations growing in the mountain tundra are

particularly sensitive to changes in climatic conditions that can cause a risk of further decrease in their number. As for the competitiveness in phytocenosis, *S. baicalensis* in all relevés registered with a coverage of 2% or less. Therefore, this species does not show high competitiveness in plant communities by implementing an ecophytocenotic strategy of patients.

The ecological area of *S. frolowii* is very narrow (74 CSU), which indicates the vulnerability of this species. The distribution of this species is limited to its specific requirements to the moisture regime and soil fertility. The vast majority of the *S. frolowii* population is observed in the range between 9–10 levels on the scale of nutrient availability and salinity and 64–66 levels on the moistening scale (Fig. 2).

In most cases (42% of relevés) *S. frolowii* coverage in plant communities is 1–5%; in 32% of cases of this species presents in plant communities with an estimated coverage of 1% or less. In 26% of cases *S. frolowii* plays a significant role in phytocenoses formation, it grows with a coverage of more than 5%, and it also dominates in plant communities or appears to be their edificatory. Almost all cenopopulations of this species from the Kuznetsk Alatau (96 relevés) are located in the optimum zone of moisture and soil quality factors. So, they grow in favorable environments and are not susceptible to such a severe risk of destabilization as a “border” population. However, not only these factors limit the abundance of *S. frolowii* in the Kuznetsk Alatau, where 45% of the populations of this species are characterized by a coverage of 4% or less (Fig. 3).

Almost half of the populations of *S. frolowii* concede the dominant position in the plant communities

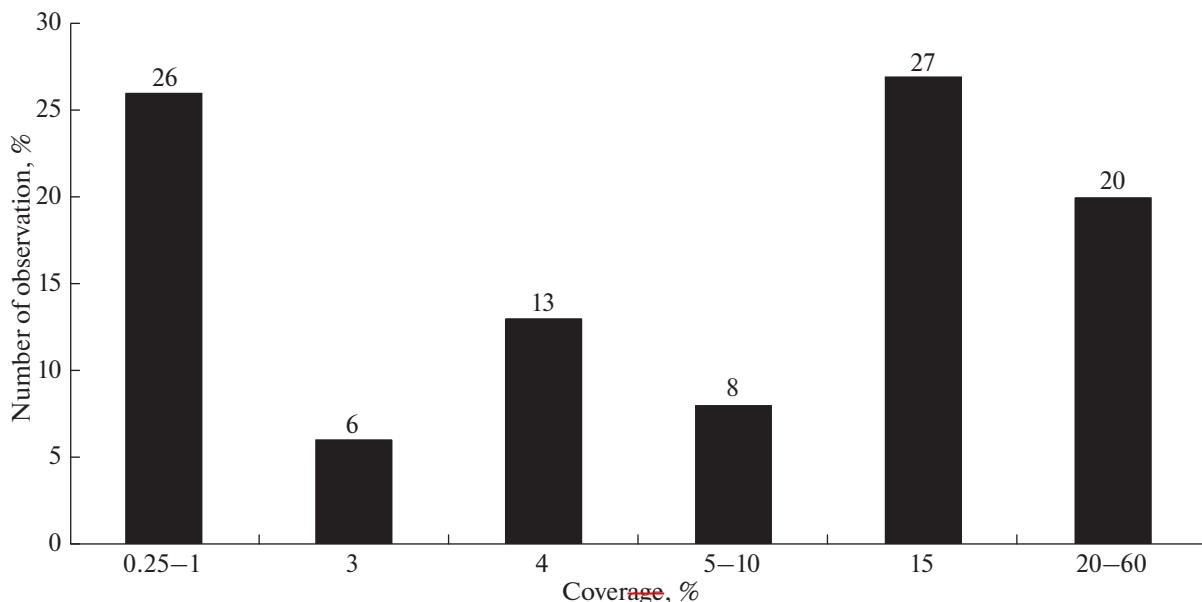


Fig. 3. Coverage of *Saussurea frolowii* in the plant communities of the Kuznetsk Alatau.

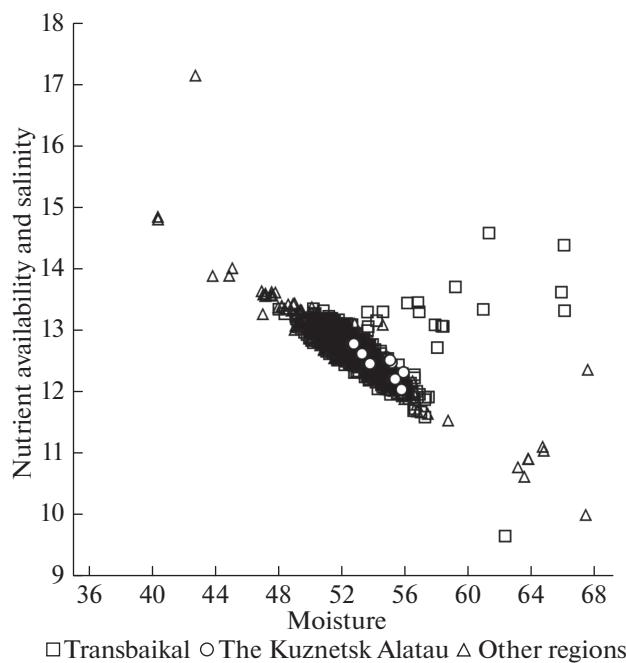


Fig. 4. Distribution of *Saussurea salicifolia* local populations in the extension of factors of moisture and nutrient availability and salinity of soil.

to representatives of mountain flora competing with this species: *Rhaponticum carthamoides* (Willd.) Iljin, *Bistorta officinalis* Delarbre, *Solidago dahurica* Kitag., and *Rumex alpestris* Jacq. The critical factor that limits the distribution and the abundance of *S. frolovii* is the influence of phytophagous insects on the generative organs of this plant species. It was found that the seed productivity in some populations of this species is significantly reduced because of insect activity. Larvae and adult weevil *Larinus sturnus* Schall. and fly-tephritid *Tephritis froloviana* Scherb consume exclusively *S. frolovii* (Shcherbakov, 2004) and eat up to 90% anthodium buds, flowers, ovules and seeds (Shurupova et al., 2014; Shurupova et al., 2015a). In addition, according to our observations, the tops of *S. frolovii* generative stems often suffer from the colonies of aphids (*Aphididae* Latreille spp.). As a result of its parasitic activity, the stem dries and an anthodium with underdeveloped seeds dropped out. It was also found that populations of *S. frolovii* are sensitive to grazing (Shurupova, 2015), as the biomorph of this species does not provide the ability of population rapid recovery (Shurupova, 2013). Accordingly, the abundance of *S. frolovii* reduced in habitats that are used for grazing.

S. salicifolia is a relatively tolerant species to the studied factors. This is also illustrated by the significant number of relevés with it; in some regions it is quite common (Serykh, 1997). Relevés of communities with *S. salicifolia* are in 10–13 levels of nutrient availability and a salinity scale that corresponds to

fairly rich soils, meadow and forest soils, loams, and leached chernozem (Rameneskii et al., 1956). On a scale of moisture, relevés are in 47–52 levels, which characterizes wet–steppe or meadow–steppe habitats on most drained dry slopes in the forest-steppe and steppe zones of the Republic of Buryatia, Irkutsk oblast, and Chita oblast. The ecological area of *S. salicifolia* is narrow (203 CSU), although it is larger in size than the other studied species (Fig. 4). The area of *S. salicifolia* is extensive (Areas of medicinal..., 1983; Ebel', 2012), the number of this species is quite high, and it is rare only on the periphery of a range which includes the lowlands of eastern macroslope of the Kuznetsk Alatau. The reason for the low occurrence of *S. salicifolia* is a small number of habitats, which are appropriate for the species within this mountain system. Sporadic locations of *S. salicifolia* in the Kuznetsk Alatau are located on the border of the geographical range in the range of 52–55 of moisture scale and 12–13 of nutrient availability and salinity scale.

In most cases (42%) *S. salicifolia* grows in plant communities sporadic. In 29% of cases, the coverage of this species is 1–2%; even more rarely (in 26% of cases), the coverage is 2–5%. *S. salicifolia* plays a significant role in the composition of plant communities, growing with coverage of more than 5% in only 2% of cases. As an edificatory this species was not registered.

According to our observations, *S. salicifolia* individuals are characterized by weak or even nonexistent vitality in the areas densely occupied by bunch grasses and sedges. Consequently, *S. salicifolia* has low competitiveness compared with those plants.

The ecological range of *S. schanginiana* is very narrow (85 CSU) (Fig. 5). Among the studied species, *S. schanginiana* shows the greatest tolerance to soil acidity. S.Yu. Lipschitz (1962) identified *S. schanginiana* var. *heteromorpha* (Turcz.) Lipsch. whose habitats are on steppe slopes and alluvial deposits of calcareous rocks in the subtaiga zone, whereas the typical variety grow in high mountains.

The association of *S. schanginiana* local populations of the Kuznetsk Alatau with a relative extension of environmental factors reveals the diversity of their ecological niches. Two locations are situated on the border of the ecological range of this species in the subtaiga zone of the Kuznetsk Alatau ($M = 54–56$; $NS = 11–13$): on the right bank of the Belyi Iyus River near the village of Efremkino and on the left side of the valley of the Kul'byurstyug River (Republic of Khakassia, Shirinskii district). In the opposite part of the ecological range, the population localized in the bald mountain zone of the Khazyr-Teren Mountain ($M = 65$; $NS = 8$) (the Republic of Khakassia, Ust'-Abakanskii district). There were not observed populations between indicated stages of ecological scales on the Kuznetsk Alatau, although the ecological range of *S. schanginiana* is fairly evenly filled with numerous

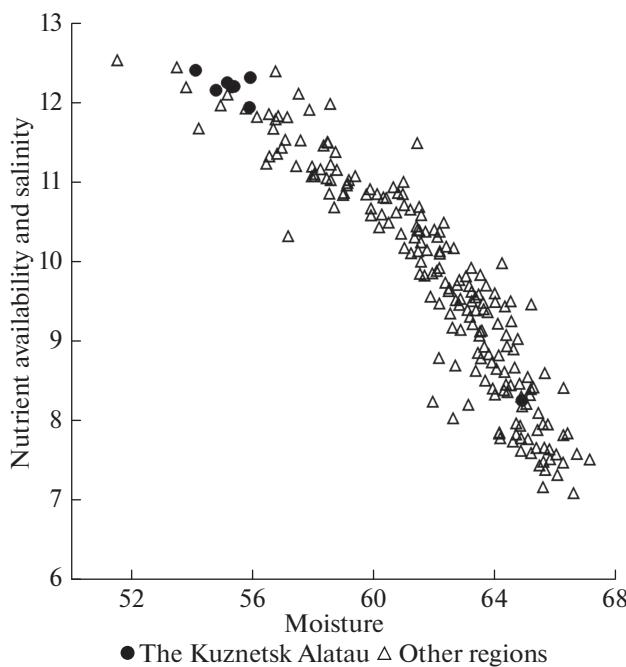


Fig. 5. Distribution of *Saussurea schanginiana* local populations in the extension of factors of moisture and nutrient availability and salinity of soil.

populations from other mountain regions of Siberia (Altai, mostly).

Probably due to the long absence of transitional ecological zones between populations of *S. schanginiana* var. *heteromorpha* of subtaiga zone and *S. schanginiana* var. *schanginiana* of high mountains, the representatives of these species differ from each other so clearly on the Kuznetsk Alatau. Thus, their population located at the boarder of the species ecological range is sensitive to changes in conditions and vulnerable.

S. schanginiana was registered with coverage from 1 to 3% in 91% of relevés, in 7% of descriptions, sporadically, and only in 2% of cases this species was met with a relatively high coverage (10–12%). For example, the unique location of *S. schanginiana* with the high abundance of this species and, therefore, the optimal conditions for its growth, is upstream of the stream Ortolyk on Kuraiskii Ridge (the Republic of Altai) and on Sangilen highlands (the Republic of Buryatia).

Thus, *S. baicalensis* is characterized by a wide geographical distribution (Malyshev, 1976; Gubanov, 1996; Serykh, 1997; Shi et al., 2011), low abundance in plant communities, and is confined to specific habitats and the weak occurrence in the Kuznetsk Alatau suitable habitats; this is confirmed by the small number of locations. Hence, based on Rabinowitz classification (1981) with modifications of Benayas et al. (1999), *S. baicalensis* is a locally endangered species in the Kuznetsk Alatau.

S. frolowii is one of the subendemics species in Altai-Sayan mountain region (Serykh, 1997), but the Kuznetsk Alatau represents only a small part of this mountain range. Therefore, within the studies on this area, the geographical distribution of this species could not be called narrow. *S. frolowii* is characterized with association to specific habitats, high abundance in communities, and significant suitable habitats occupancy (which are confirmed by the large number of locations in the Kuznetsk Alatau). Although for the Altai-Sayan mountain region in general this species can be attributed to the “endemic indicator” type of rarity, for the Kuznetsk Alatau *S. frolowii* it is an indicator species, occurring only in the meadows and woodlands of the subalpine zone.

An extensive ecological range, a narrow ecological niche, and a low abundance in communities are inherent for *S. salicifolia*. The rarity of this species in the Kuznetsk Alatau is of a peripheral character; there are few habitats and suitable environmental conditions for this species within this mountain system. Therefore, we assume that *S. salicifolia* is characterized by high suitable habitat occupancy. According to the classification of Rabinowitz (1981) with modifications (Benayas et al., 1999), on the Kuznetsk Alatau this species is also an indicator, occurring in the least moisturizing habitats with the richest soils.

S. schanginiana is characterized by an extensive geographical distribution (Red Book..., 2000, 2008a, b, 2009), but by very narrow ecological range. Herewith, the abundance of this species in communities is low, as is the number of locations in the Kuznetsk Alatau, which indicates the low occupancy of suitable habitats. Therefore, within this mountain system the species is locally endangered.

CONCLUSIONS

Although the rarity types have no direct connection with the categories of conservation and form a part of scientific terminology, the use of this classification can be useful for plant conservationists, because it helps structure the available information on geographical distribution, ecology, and competitiveness in phytocenosis of rare species. The application of databases (on IBIS example) expands the information content of species indicator values analysis by the method of ecological scales with the concept of ecological range (ecological niche), allowing one to evaluate species vulnerability and their rarity types. Although the classification of types of rarity does not affect such important criteria of vulnerability as a threat to species survival and the speciality of biology and population status, it is designed to draw attention of plant conservationists to species that are not common and ordinary. Obviously, most attention from the biodiversity conservation should be focused on stenotopic species, which are found in low abundance in a small number

of locations. These species are *S. baicalensis* and *S. schanginiana* among the studied *Saussurea* species. We recommend including these species in the list of protected species of Kemerovo oblast, because they are registered in only one location on its territory: the Bolshoi Kanym mountain (Buko, 2002). *S. frolowii* and *S. salicifolia*, are characterized by low tolerance to moisture and soil quality, but they also are vulnerable in the Kuznetsk Alatau. Arranging special actions for the conservation of these species of *Saussurea* in the Republic of Khakassia is more difficult because the decision to protect is under administrative-level supervision. The Republic of Khakassia occupies not only the eastern macroslope of the Kuznetsk Alatau, but also a part of Nazarovsko-Minusinsk intermountain depression and the Western Sayan; we have no reason to estimate the vulnerability of *S. baicalensis*, *S. frolowii*, *S. salicifolia*, and *S. schanginiana* across the whole republic. It may be necessary to enter the mode of protection of these species in the administrative districts of the Republic of Khakassia, located in the Kuznetsk Alatau

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REFERENCES

- Albright, T.P., Chen, H., Chen, L., and Guo, Q., The ecological niche and reciprocal prediction of the disjunct distribution of an invasive species: the example of *Ailanthus altissima*, *Biol. Invasions*, 2010, vol. 12, no. 8, pp. 2413–2427.
- Alley, T.R., Completion theory, evolution, and the concept of an ecological niche, *Acta Biotheor.*, 1982, vol. 31, no. 3, pp. 165–179.
- Arealy lekarstvennykh i rodstvennykh im rastenii SSSR (Atlas) (Areals of Medical and Related Plants in Soviet Union: Atlas), Shmidt, V.M., Ed., Leningrad: Leningr. Gos. Univ., 1983.
- Begon, M., Harper, J.L., and Townsend, C.R., *Ecology: Individuals Populations and Communities*, Oxford: Blackwell, 2006, 4th ed.
- Buko, T.E., Conspectus of flora of higher vascular plants in Kuznetsk Ala-Tau Nature Reserve, in *Botanicheskie issledovaniya Sibiri i Kazakhstana* (Botanic Studies in Siberia and Kazakhstan), Barnaul: Altai. Gos. Univ., 2002, no. 8, pp. 35–53.
- Bulokhov, A.D., *Fitoindikatsiya i ee prakticheskoe primenie (Phytoindication and Its Practical Use)*, Bryansk: Bryansk. Gos. Univ., 2004.
- Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P., Villéger, S., and Mouquet, N., Defining and measuring ecological specialization, *J. Appl. Ecol.*, 2010, vol. 47, no. 1, pp. 15–25.
- Diekmann, M., Species indicator values as an important tool in applied plant ecology—a review, *Basic Appl. Ecol.*, 2003, vol. 4, no. 6, pp. 493–506.
- Ebel', A.L., *Konspekt flory severo-zapadnoi chasti Altae-Sayanskoi provintsii (The List of Flora of the Northwestern Part of Altai-Sayan Province)*, Kemerovo: Irbis, 2012.
- Ellenberg, H., *Landwirtschaftliche Pflanzensoziologie. I. Unkrautgemeinschaften als Zeiger für Klima und Boden*, Stuttgart: Ulmer, 1950.
- Ellenberg, H., *Zeigerwerte der Gefäßpflanzen Mitteleuropas*, *Scr. Geobot.*, 1974, vol. 9.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., and Paulissen, D., *Zeigerwerte von Pflanzen in Mitteleuropa*. Ed. 2, *Scr. Geobot.*, 1992, vol. 18.
- Faber-Langendoen, D., Nichols, J., Master, L., Snow, K., Tomaino, A., Bittman, R., Hammerson, G., Heidel, B., Ramsay, L., Teucher, A., and Young, B., *NatureServe Conservation Status Assessments: Methodology for Assigning Ranks*, Arlington: NatureServe, 2012.
- Frank, D. and Klotz, S., *Biologisch-Ökologische Daten zur Flora der DDR*, Halle: Wiss. Beitr. Martin-Luther Univ., 1990.
- Friberg, M., Bergman, M., Kullberg, J., Wahlberg, N., and Wiklund, C., Niche separation in space and time between two sympatric sister species—a case of ecological pleiotropy, *Evol. Ecol.*, 2008, vol. 22, no. 1, pp. 1–18.
- Gaston, K., *Rarity*, London: Chapman & Hall, 1994.
- Given, D. and Williams, P.A., *Conservation of Chatham Island Flora and Vegetation*, Christchurch: Bot. Div., Dep. Sci. Ind. Res., 1984.
- Gleason, H.A., The structure and development of the plant associations, *Bull. Torrey Bot. Club*, 1917, vol. 44, no. 10, pp. 463–481.
- Gleason, H.A., The individualistic concept of the plant association, *Bull. Torrey Bot. Club*, 1924, vol. 53, pp. 7–26.
- Griscom, H.P. and Griscom, B.W., Evaluating the ecological niche of American chestnut for optimal hybrid seedling reintroduction sites in the Appalachian ridge and valley province, *New Forest*, 2012, vol. 43, no. 4, pp. 441–455.
- Gubanov, I.A., *Konspekt flory Vneshnei Mongolii (sosudistye rasteniya)* (The List of flora of External Mongolia: Vascular Plants), Kamelin, R.V., Ed., Moscow: Valang, 1996.
- Holt, R.D., Rarity and evolution: some theoretical considerations, in *The Biology of Rarity Causes and Consequences of Rare-Common Differences Population and Community*, Kunin, W.E. and Gaston, K.J., Eds., London: Chapman & Hall, 1997, pp. 209–234.
- Hundt, R., Ökologisch-geobotanische Untersuchungen an Pflanzen der mitteleuropäischen Wiesenvegetation, *Bot. Stud.*, 1966, no. 16, pp. 1–176.
- Hutchinson, G.E., Concluding remarks, *Cold Spring Harbor Symp. Quant. Biol.*, 1957, vol. 22, pp. 415–427.

- Irfan-Ullah, M., Amarnath, G., Murthy, M.S.R., and Peterson, A.T., Mapping the geographic distribution of *Aglaia bourdillonii* Gamble (Meliaceae), an endemic and threatened plant, using ecological niche modeling, *Biodiversity Conserv.*, 2007, vol. 16, no. 6, pp. 1917–1925.
- Komarov, A.S. and Subkova, E.V., Distribution pattern of ecological niches in the plant forest communities during succession, *Matem. Biol. Bioinf.*, 2012, vol. 7, no. 1, pp. 152–161.
- Korolyuk, A.Yu., Ecological maximums of the plants of Southern Siberia, in *Botanicheskie issledovaniya Sibiri i Kazakhstana* (Botanical Studies of Siberia and Kazakhstan), Barnaul: Irbis, 2006, no. 12, pp. 3–28.
- Korolyuk, A.Yu., Troeva, E.I., Cherosov, M.M., Gogoleva, P.A., and Mironova, S.I., *Ekologicheskaya otsenka flory i rastitel'nosti tsentral'noi Yakutii* (Ecological Assessment of Flora and Vegetation of Central Yakutia), Yakutsk: Yakut. Nauch. Tsentr, Sib. Otd., Ross. Akad. Nauk, 2005.
- Krasnaya kniga Altaiskogo kraja. Redkie i nakhodyashchiesya pod ugrozoi ischeznoveniya vidy rastenii* (The Red Data Book of Altai Krai: Rare and Endangered Plant Species), Barnaul: Altai, 2006.
- Krasnaya kniga Amurskoi oblasti: redkie i nakhodyashchiesya pod ugrozoi ischeznoveniya vidy zhivotnykh, rastenii i gribov* (The Red Data Book of Amur Oblast: Rare and Endangered Species of the Animals, Plants, and Fungi), Blagoveshchensk: Blagoveshch. Gos. Pedagog. Univ., 2009.
- Krasnaya kniga Chukotskogo avtonomnogo okruga. Tom 2. Redkie i nakhodyashchiesya pod ugrozoi ischeznoveniya vidy rastenii (pokrytosemennye, paporotnikovidnye, plaunovidnye, mokhoobraznye, lishainiki, griby)* (The Red Data Book of Chukotka Autonomous District, Vol. 2: Rare and Endangered Plant Species: Angiosperms, Ferns, Mosses, Lichen, and Fungi), Magadan: Dikii Sever, 2008b.
- Krasnaya kniga Kemerovskoi oblasti: redkie i nakhodyashchiesya pod ugrozoi ischeznoveniya vidy rastenii i gribov* (The Red Data Book of Kemerovo Oblast: Rare and Endangered Species of the Plants and Fungi), Kemerovo: Kemerovsk. Knizhn. Izd., 2000.
- Krasnaya kniga Kemerovskoi oblasti. Tom 1. Redkie i nakhodyashchiesya pod ugrozoi ischeznoveniya vidy rastenii i gribov* (The Red Data Book of Kemerovo Oblast, Vol. 1: Rare and Endangered Species of the Plants and Fungi), Kemerovo: Aziya Print, 2012, 2nd ed.
- Krasnaya kniga Khabarovskogo kraja: redkie i nakhodyashchiesya pod ugrozoi ischeznoveniya vidy rastenii i zhivotnykh* (The Red Data Book of Khabarovsk Krai: Rare and Endangered Species of the Plants and Animals), Khabarovsk: Priamurskie Vedomosti, 2008a.
- Krasnaya kniga Krasnoyarskogo kraja. Tom 2. Redkie i nakhodyashchiesya pod ugrozoi ischeznoveniya vidy dikorastushchikh rastenii i gribov* (The Red Data Book of Krasnoyarsk Krai, Vol. 2: Rare and Endangered Species of the Wild Plants and Fungi), Krasnoyarsk: Znak, 2012, 2nd ed.
- Krasnaya kniga Respubliki Khakasiya: redkie i ischezayushchie vidy rastenii i gribov* (The Red Data Book of Khakassia Republic: Rare and Endangered Species of the Plants and Fungi), Novosibirsk: Nauka, 2002.
- Krasnaya kniga Respubliki Sakha (Yakutiya). Tom 1. Redkie i nakhodyashchiesya po ugrozoi ischeznoveniya vidy rastenii i gribov* (The Red Data Book of Sakha Republic (Yakutia), Vol. 1: Rare and Endangered Species of the Plants and Fungi), Yakutsk: Sakhapoligrafizdat, 2000.
- Kuminova, A.V., *Rastitel'nyi pokrov Altaya (Vegetation Cover of Altai)*, Novosibirsk: Sib. Otd., Akad. Nauk SSSR, 1960.
- Landolt, E., *Ökologische Zeigerwerte zur Schweizer Flora, Veröff. Geobot. Inst. Eidgen. Tech. Hochsch., Zürich*, 1977, vol. 64, pp. 1–208.
- Landolt, E., Bäumler, B., Erhardt, A., Hegg, O., Klötzli, F., Lämmler, W., Nobis, M., Rudmann-Maurer, K., Schweingruber, F.H., Theurillat, J.-P., Urmí, E., Vust, M., and Wohlgemuth, T., *Flora Indicativa: Ökologische Zeigerwerte und Biologische Kennzeichen zur Flora der Schweiz und der Alpen*, Bern: Haupt Verlag, 2010.
- Lindenmayer, D. and Burgman, M., *Practical Conservation Biology*, Collingwood: Commonw. Sci. Ind. Res. Org., 2006.
- Lipshits, S.Yu., Genus *Saussurea* DC, in *Flora SSSR (Flora of Soviet Union)*, Moscow: Akad. Nauk SSSR, 1962, vol. 27, pp. 361–535.
- Malyshev, L.I., *Vysokogornaya flora Vostochnogo Sayana (High-Altitude Flora of Eastern Sayan Mountains)*, Moscow: Nauka, 1965.
- Nekratova, N.A. and Nekratov, N.F., *Lekarstvennye rasteniya Altai-Sayanskoi gornoj oblasti. Resursy, ekologiya, tsenokompleksy, populjatsionnaya biologiya, rational'noe ispol'zovanie* (Medical Plants of Altai-Sayan Mountain Region: Resources, Ecology, Cenoses, Population Biology, and Rational Use), Tomsk: Tomsk. Gos. Univ., 2005.
- Pocheville, A., The ecological niche: history and recent controversies, in *Handbook of Evolutionary Thinking in the Sciences*, Heams, T., Huneman, P., Lecointre, G., and Silberstein, M., Eds., Dordrecht: Springer-Verlag, 2014, pp. 547–586.
- Rabinowitz, D., Seven forms of rarity, in *The Biological Aspects of Rare Plant Conservation*, Syngle, H., Ed., Chichester: Wiley, 1981, pp. 205–217.
- Ramenskii, L.G., Comparative ecological analysis of the plant communities, *Dnevnik XII S"ezda russkikh estestvoispytatelei i vrachei* (The Diary of XII Congress of Russian Naturalists and Physicians), Moscow, 1910, no. 7, pp. 389–390.
- Ramenskii, L.G., *Vvedeni v kompleksnoe pochvenno-geobotanicheskoe issledovanie zemel'* (Introduction to the Complex Soil-Geobotanical Study of the Lands), Moscow: Sel'khozgiz, 1938.
- Ramenskii, L.G., *Izbrannye raboty: Problemy i metody izuchenija rastitel'nogo pokrova* (Selected Research Works: Problems and Methods in the Study of Vegetation Cover), Leningrad: Nauka, 1971.
- Ramenskii, L.G., Tsatsenkin, I.I., Chizhikov, O.N., and Antipin, N.A., *Ekologicheskaya otsenka kormovykh ugodii po rastitel'nomu pokrovu* (Ecological Assessment of Fodder Resources by Vegetation Cover), Moscow: Sel'khozgiz, 1956.
- Rey Benayas, J., Schneiner, S., García Sánchez-Colomer, M., and Levassor, C., Commonness and rarity: theory and application of a new model to Mediterranean mon-

- tane grasslands, *Conserv. Ecol.*, 1999, vol. 3, no. 1, p. 5. <http://www.consecol.org/vol3/iss1/art5>.
- Sanchez, A.C., Osborne, P.E., and Haq, N., Identifying the global potential for baobab tree cultivation using ecological niche modelling, *Agrofor. Syst.*, 2010, vol. 80, no. 2, pp. 191–201.
- Seledets, V.P., Ecological ranges of plant species in the continental and Ocean regions of Asian Russia, *Contemp. Probl. Ecol.*, 2009, vol. 2, no. 4, pp. 314–321.
- Seledets, V.P., The concept of the ecological range of the species in the botanical studies in the Russian Far East, *Byull. Bot. Sada-Inst., Dal'nost. Otd., Ross. Akad. Nauk*, 2010, no. 7, pp. 23–38.
- Seledets, V.P. and Probatova, N.S., *Ekologicheskii areal vida u rastenii (Ecological Areal of the Plant Species)*, Vladivostok: Dal'nauka, 2007.
- Serykh, G.I., Genus *Saussurea* DC, in *Flora Sibiri. Tom 13. Asteraceae (Compositae)* (Flora of Siberia, Vol. 13: Asteraceae (Compositae)), Novosibirsk: Nauka, 1997, pp. 180–209.
- Shcherbakov, M.V., Tephritid flies (Tephritidae, Diptera) from the central part of Kuznetsk Ala-Tau, *Entomol. Obozr.*, 2002, vol. 81, no. 2, pp. 460–487.
- Shi, Z., Raab-Straube, E., Greuter von, W., and Martins, L., Cardueae, in *Flora of China*, Vols. 20–21: *Asteraceae*, Wu, Z.Y., Raven, P.H., and Hong, D.Y., Eds., St. Louis: Miss. Bot. Garden, 2011, pp. 42–194.
- Shurupova, M.N., Ecological and biological features of *Saussurea frolovii* Ledeb. in Kuznetsk Ala-Tau, *Mater. mezhregional'noi nauchno-prakticheskoi konferentsii "Bioraznoobrazie Altai-Sayanского екорегиона: изучение и сохранение в системе ООПТ,"* Kyzyl, 27 iyunya–1 iyulya, 2013 g. (Proc. Interregional Sci.-Pract. Conf. “Biodiversity of Altai-Sayan Ecological Region: Study and Preservation in the System of Strictly Protected Natural Territories,” Kyzyl, June 27–July 1, 2013), Kyzyl: Tyvapoligraf, 2013, pp. 107–111.
- Shurupova, M.N., Ecology and biology of rare species of genus *Saussurea* DC. from Kuznetsk Ala-Tau, *Extended Abstracts of Cand. Sci. (Biol.) Dissertation*, Tomsk, 2015.
- Shurupova, M.N. and Gureyeva, I.I., Ontogenesis and structure of *Saussurea schanginiana* (Asteraceae) populations in vicinities of Efremkino village (Khakassia Republic), *Trudy IX mezhdunarodnoi konferentsii po ekologicheskoi morfologii rastenii, posvyashchennoi 100 letiyu so dnya rozhdeniya I.G. Serebryakova* (Proc. IX Int. Conf. on Ecological Morphology of the Plants Dedicated to the 100th Anniversary of I.G. Serebryakov), Viktorov, V.P., Ed., Moscow, 2014, vol. 2, pp. 476–479.
- Shurupova, M.N., Gureyeva, I.I., and Nekratova, N.A., Ontogenesis and population structure of *Saussurea salicifolia* (Asteraceae) from Kuznetsk Ala-Tau, *Rast. Resur.*, 2014a, vol. 50, no. 2, pp. 205–215.
- Shurupova, M.N., Gureyeva, I.I., and Nekratova, N.A., Biomorphology and ontogenesis of *Saussurea baicalensis* from Kuznetsk Ala-Tau, *Mater. Vseross. nauchnoi konferentsii s mezhdunarodnym ucheстием "Fundamental'naya i prikladnaya biomorfologiya v botanicheskikh i ekologicheskikh issledovaniyah"* (Proc. All-Russ. Sci. Conf. with Int. Participation “Fundamental and Applied Biomorphology in Botanical and Ecological Studies”), Kirov, 2014b, pp. 153–155.
- Shurupova, M.N., Gureyeva, I.I., and Nekratova, N.A., Seed production and germination of three rare *Saussurea* species in the Kuznetsk Ala-Tau, *Adv. Environ. Biol.*, 2014c, vol. 8, no. 21, pp. 396–402.
- Shurupova, M.N., Gureyeva, I.I., and Nekratova, N.A., *Specific reproduction of rare species of genus Saussurea (Asteraceae) in Kuznetsk Ala-Tau*, *Vestn. Tomsk. Gos. Univ., Biol.*, 2015, vol. 29, no. 1, pp. 86–102.
- Solano, E. and Feria, T.P., Ecological niche modeling and geographic distribution of the genus *Polianthes* L. (Aga-vaceae) in Mexico: using niche modeling to improve assessments of risk status, *Biodiversity Conserv.*, 2007, vol. 16, no. 6, pp. 1885–1900.
- Tanzybaev, M.B., Soil cover, in *Rastitel'nyi pokrov Khakassii (Vegetation Cover of Khakassia)*, Kuminov, A.V., Ed., Novosibirsk: Nauka, 1976, pp. 30–39.
- Thuiller, W., Gasso, N., Pino, J., and Vila, M., Ecological niche and species traits: key drivers of regional plant invader assemblages, *Biol. Invasions*, 2012, vol. 14, no. 9, pp. 1963–1980.
- Troeva, E.I., Zverev, A.A., Korolyuk, A.Yu., and Cherosov, M.M., Ecological scales of flora and microbiota of Yakutia, in *Flora Yakutii: geograficheskie i ekologicheskie aspekty (Flora of Yakutia: Geographical and Ecological Aspects)*, Egorova, A.A., Ed., Novosibirsk: Nauka, 2010, pp. 114–150.
- Tsatsenkin, I.A., *Ekologicheskie shkaly dlya rastenii pastbishch i senokosov gornykh i ravninnnykh raionov Srednei Azii, Altaya i Urala (Ecological Scales for the Pasture and Hayfield Plants of the Mountain and Plain Regions of Central Asia, Altai, and Ural)*, Dushanbe: Donish, 1967.
- Tsatsenkin, I.A., Dmitrieva, S.I., Belyaeva, N.V., and Savchenko, I.V., *Metodicheskie ukazaniya po ekologicheskoi otsenke kormovykh ugodiий lesostepnoi i stepnoi zon Sibiri po rastitel'nomu pokrovu* (Methodological Recommendation for Ecological Assessment of Fodder Resources of Forest-Steppe and Steppe Zones of Siberia by Vegetation Cover), Moscow: Vses. Nauchno-Issled. Inst. Kormov im. V.R. Vil'yamsa, 1974.
- Tsatsenkin, I.A., Dmitrieva, S.I., and Savchenko, I.V., *Metodicheskie ukazaniya po ekologicheskoi otsenke kormovykh ugodiий tundrovoi i lesnoi zon Sibiri i Dal'nego Vostoka po rastitel'nomu pokrovu* (Methodological Recommendation for Ecological Assessment of Fodder Resources of Tundra and Forest Zones of Siberia and Far East by Vegetation Cover), Moscow: Vses. Nauchno-Issled. Inst. Kormov im. V.R. Vil'yamsa, 1978.
- Tsyganov, D.N., *Fitoindikatsiya ekologicheskikh rezhimov v podzone khvoino-shirokolistvennykh lesov (Phytoindication of Ecological Regimes in Subzone of Coniferous-Broad-Leaved Forests)*, Moscow: Nauka, 1983.
- Zhukova, L.A., Methods for analysis of ecological valence and eurybiotic plant species, in *Mater. VII Vseross. populyatsionnogo seminara "Metody populyatsionnoi biologii"* (Proc. VII All-Russ. Population Seminar “Practical Population Biology”), Syktyvkar, 2004, part 1, pp. 75–76.
- Zhukova, L.A., Dorogova, Yu.A., Turmukhametova, N.V., Gavrilova, M.N., and Polyanskaya, T.A., *Ekologiches-*

- kie shkaly i metody analiza ekologicheskogo raznootraziya rastenii (Ecological Scales and Analysis of Ecological Diversity of the Plants)*, Yoshkar-Ola: Mariisk. Gos. Tekh. Univ., 2010.
- Zlobin, Yu.A., Sklyar, V.G., and Klimenko, A.A., *Populyatsii redkikh vidov rastenii: teoreticheskie osnovy i metodika izucheniya. Monografiya (Population of Rare Plant Species: Theretical Principles and Study Method. Monograph)*, Sumy: Universitetskaya Kniga, 2013.
- Zubkova, E.V., Ratio dynamics of implemented ecological niches of the plants in communities during succession, *Izv. Samar. Nauch. Tsentra, Ross. Akad. Nauk*, 2009, vol. 11, no. 1 (7), pp. 1634–1639.
- Zverev, A.A., *Informatsionnye tekhnologii v issledovaniyakh pokrova: uchebnoe posobie (Implementation of Information Technologies for Analysis of Vegetation Cover: Manual)*, Tomsk: TML-Press, 2007.
- Zverev, A.A., Phytoindication analysis: automated approach, *Mater. VIII mezhdunarodnoi nauchno-prakticheskoi konferentsii "Problemy botaniki Yuzhnoi Sibiri i Mongoli" (Proc. VIII Int. "Problems in Botany of Southern Siberia and Mongolia")*, Barnaul: Artika, 2009, pp. 344–347.
- Zverev, A.A., Use of agreement indices for ecological analysis of vegetation, *Mater. V Vseross. konferentsii "Flora i rasitel'nost' Sibiri i Dal'nego Vostoka" (Proc. V All-Russian Conf. "Flora and Vegetation of Siberia and Far East")*, Krasnoyarsk, 2011, vol. 2, pp. 311–318.
- Zverev, A.A., Use of equivalence classes and factor sets in the analysis of botanical data, *Contemp. Probl. Ecol.*, 2012, vol. 5, no. 2, pp. 165–173.
- Zverev, A.A. and Babeshina, L.G., Evaluation of habitat conditions of sphagnum moss of the West Siberian Plain by the key ecological factors: objects, materials, and analysis methods, *Vestn. Tomsk. Gos. Univ., Biol.*, 2009, no. 325, pp. 167–173.

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