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Assessment of state of *Dactylorhiza fuchsii* (Orchidaceae) populations from the Altai mountains of Kazakhstan

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Abstract. *Sumbembayev AA, Tergenbaeva ZHT, Kudabayeva GM, Tashmetova RS, Genievskaya YA, Szlachetko DL. 2022. Title. Biodiversitas 23: 4385-4399.* The article presents the results of studying the current state of populations of a rare species - *Dactylorhiza fuchsii* in the Kazakhstan Altai. As a result of expeditionary studies, four main regions were identified, which were represented by 12 populations. Floristic plasticity according to the Jaccard coefficient (12-24%) showed a high heterogeneity of the studied populations. The cluster population dendrogram showed a clear dependence of the floristic composition of accompanying species on geographic location in terms of species similarity and difference of communities. External similarity was studied according to 10 morphometric features. The PCA analysis shows that the external structure is influenced by vertical zoning. Pearson's correlation analysis showed a stable direct and inverse dependence of morphometric characteristics on some environmental conditions (0.74-0.95). According to the data ANOVA disperse analysis, among studied environmental factors, soil nutrient richness (N) and humidity (F) had demonstrated the broadest significant effects (P-values from < 2e-16 to 0.001 for N and from 8.02e-09 to 0.02 for F) on plants morphology influencing eight out of ten morphological traits. Distribution regions of *D. fuchsii* have low vitality, and most populations are characterized as depressed. The results harmoniously complement the fundamental research on the state of *D. fuchsii* populations throughout the distribution range of the species.

Keywords: Ecological optimum, floristic composition, morphometric characteristics, Red Data Book species

INTRODUCTION

Conservation of biological diversity of plants is a global task of preserving the human habitat. The strategy for the conservation of rare and endangered plants should be based on the identification of regularities in the existence of species in natural populations (Kupriyanov et al. 2019).

Dactylorhiza fuchsii (Druce) Soo is a hygro-mesophyte with a Euro-Siberian range that grows in wet meadows, marshy lowlands, and short grass communities (Vahrameeva et al. 2014). Kazakhstan distribution points of *D. fuchsii* are the peripheral residual part of the Siberian mountain-taiga range of the species. It is a rare species with a declining range (Red Book of Kazakhstan, 2014; Gutowski 1990). *D. fuchsii* is included under Annex B of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). The species is protected at national level in Belgium and Luxembourg and at regional level in France (IUCN 2020). In Kazakhstan, it is under protection in nature reserves (Perezhogin 2017) and in national parks (Sultangazina et al. 2013). In the Kazakhstan Altai, it often rises to the middle mountain belt of dark coniferous forests (Danilova and Sumbembayev 2021). The species always prefers humus-rich soils. Rarity: critically endangered - CR (IUCN 2020).

Many studies have been carried out concerning the biology of *D. fuchsii* in anatomy (Aybeke et al 2010; Naczk et al 2010), morphometry and biostatistics (Dufrêne et al. 1991; Tyteca and Gathoye 1999; Sumbembayev et al. 2021), ontogenesis (Vakhrameeva 2006; Jacquemyn et al. 2012), micropropagation (Jakobsone 2008; Jakobsone et al. 2010), geographic distribution (Đorđević et al. 2014), and genetics (De Hert et al. 2012; Box et al. 2012; Efimov et al. 2016; Wróblewska et al. 2019). At the same time, a limited number of population studies of the species were carried out (Dufrêne et al. 1991; Kotukhov et al. 2018; Bateman and Denholm 1989; Janečková et al. 2006; Kirillova and Kirillov 2013; Taraška 2021; Kosolapova et al. 2021), especially in the peripheral part of the range. Special studies on the study of populations of *D. fuchsii*, the ecological characteristics of communities and the floristic composition of these populations in the territory of the Kazakhstan part of the Altai mountainous country have not been previously carried out.

The main goal of this study is the ecological and population survey of *D. fuchsii* in the Kazakhstan part of the Altai mountainous country. To do this, it was necessary to determine the ecological optimum and plasticity of the species in the surveyed communities based on the similarity and difference in the floristic composition. To study the current state of *D. fuchsii* populations and establish an ecological optimum, the main tasks were: to determine the similarities of plant communities, the degree of renewal, the establishment of the floristic composition, the analysis of vitality, the main limiting factors and the dependence of morphometric characteristics on environmental conditions.

MATERIALS AND METHODS

The studies were carried out in the Kazakh part of the Altai Mountains, which is a fragment of the Sayan-Altai Mountains (Ponomarev and Kharuk 2016). The climatic conditions of the region are formed with its location in the center of the Eurasian continent with the same distance from the oceans, the proximity of the deserts of Mongolia and Central Asia, as well as the position in the system of continental-ocean transport of air masses (Bajtulin and Kotukhov 2021). The survey of the territory was carried out by the route-reconnaissance method (Peet et al. 1998) covering the typical habitats of the Kazakhstan part of the Altai Mountains.

To characterize the ecological features of *D. fuchsii* populations, we used descriptions of the levels of ecological factors on the scales of illumination (L), humidity (F), soil acidity (R), and soil nutrient richness (N) introduced by Landolt (1977). Determining the levels of ecological scales was carried out directly on the spot, in specific natural habitats. When studying the external morphometry of the generative individuals of the studied populations, the following were determined: the plant height, the number of leaves, the length and diameter of the inflorescence, the length of the peduncle, the length and width of stem leaves, the length and width of basal leaves, and the number of flowers in inflorescence. These indicators were determined in 20 repetitions for each population. Latin names of plants are given according to POWO (2022). The phylogenetic plant classification system is indicated according to Takhtajyan (2009). Species abundance was indicated on a Braun-Blanquet scale (1964). Species and genera in families (Table S1) are arranged alphabetically.

To establish similarities in the rank structure of the spectrum of 10 leading families of accompanying species, the Spearman rank correlation coefficient was used (Spearman 1904). The correlation between morphometric traits and environmental factors was calculated using Pearson's linear correlation coefficient (Pearson 1895). Data for principal component analysis (PCA), ANOVA, correlation analysis, and construction of a dendrogram of the similarity of populations (cluster analysis) were processed using the statistical software R-4.1.3 (www.R-project.org). The floristic similarity of accompanying species for the studied populations was calculated using the Jaccard formula (1901):

$$Kj = \frac{c}{a+b-c}$$

Where; *a*: the number of species in one population, *b*: the number of species in another population, *c*: the number of species common to two populations.

The construction of a cluster dendrogram of populations by species similarity was carried out in the GenAlEx software, version 6.5 (Peakall and Smouse 2012). To do this, the entire list of flora species was classified by population, the presence of a species in a population was marked as "1", the absence of a species as "0". Clustering was carried out using the Neighbor-joining clustering method.

The assessment of the vitality composition of the studied populations was carried out using two methods: the method for determining the vitality of populations (Q) by Zlobin (1989) and the vitality index (IVC) proposed by Ishbirdin and Ishmuratova (2004). As a result of expeditionary surveys, 12 populations were identified from 4 main regions: Sarymsacty, Buchtarma, West Altai and Azutau (Figure 1). Twelve populations (Pop) were recorded under different ecological and phytocenotic conditions (Table 1).

RESULTS AND DISCUSSION

The basis for the development of measures for the protection and conservation of rare species is the assessment of their condition in modern plant communities at the population level (Egorova and Suleimanova 2021). As a result of expeditionary studies, it was found that the flora of accompanying species for *D. fuchsii* populations in the Kazakhstan part of the Altai mountains includes 251 species (Table 2), belonging to 49 families and 155 genera (Table S1). Typical marker species are *Betula verrucosa* Ehrh., *Juncus compressus* Jacq., *Poa palustris* L., *Poa pratensis* L., *Filipendula ulmaria* (L.) Maxim., *Geum rivale* L., *Sanguisorba officinalis* L. Populations occupy moist meadows, edges of birch and mixed forests, valleys of rivers and streams, in areas with stable moisture and a rich humus substrate.

Populations are of different ages, with weak seed renewal. Of the 12 populations, only Pop 2, Pop 5 and Pop 9 are the most stable in terms of the ratio of generative - vegetative individuals and the level of self-renewal (Figure 2). The first task in assessing population diversity was to establish *D. fuchsii* plasticity. For this, a study was carried out on the similarity and difference of the studied regions based on the Jaccard coefficient. It was found that the floral composition similarity of the examined regions varies within 12-24% (Table 3).

The cluster dendrogram based on floral similarity and difference in region flora (Table S1) showed the proximity of Buchtarma and Azutau regions, which form cluster 1. Sarymsacty and West Altai regions, rich enough in floral diversity, form a separate cluster 2 (Figure 3).

The second important aspect of the study was the study of the external morphometry of generative individuals of 12 *D. fuchsii* populations according to 10 morphometric characters (Table 4). The analysis of ranking by external similarity, presented in the cluster dendrogram (Figure 4), graphically showed patterns in the structural arrangement. So, Pop 1 and Pop 4 related to Sarymsacty and Buchtarma regions form a separate cluster 2. Pop 5, Pop 6, Pop 7, Pop 8, Pop 9, Pop 10, Pop 11 and Pop 12 belonging to West Altai and Azutau regions form separate clusters 1 and 3. Despite the geographical proximity of Sarymsacty and Buchtarma regions to Azutau, the relationship in terms of external morphometry between them has not been established. At the same time, West Altai and Azutau, which are the most distant geographically, show stable similarity in morphometry. It can be assumed that the external structure is more influenced by vertical zoning, and not by geographical disunity.

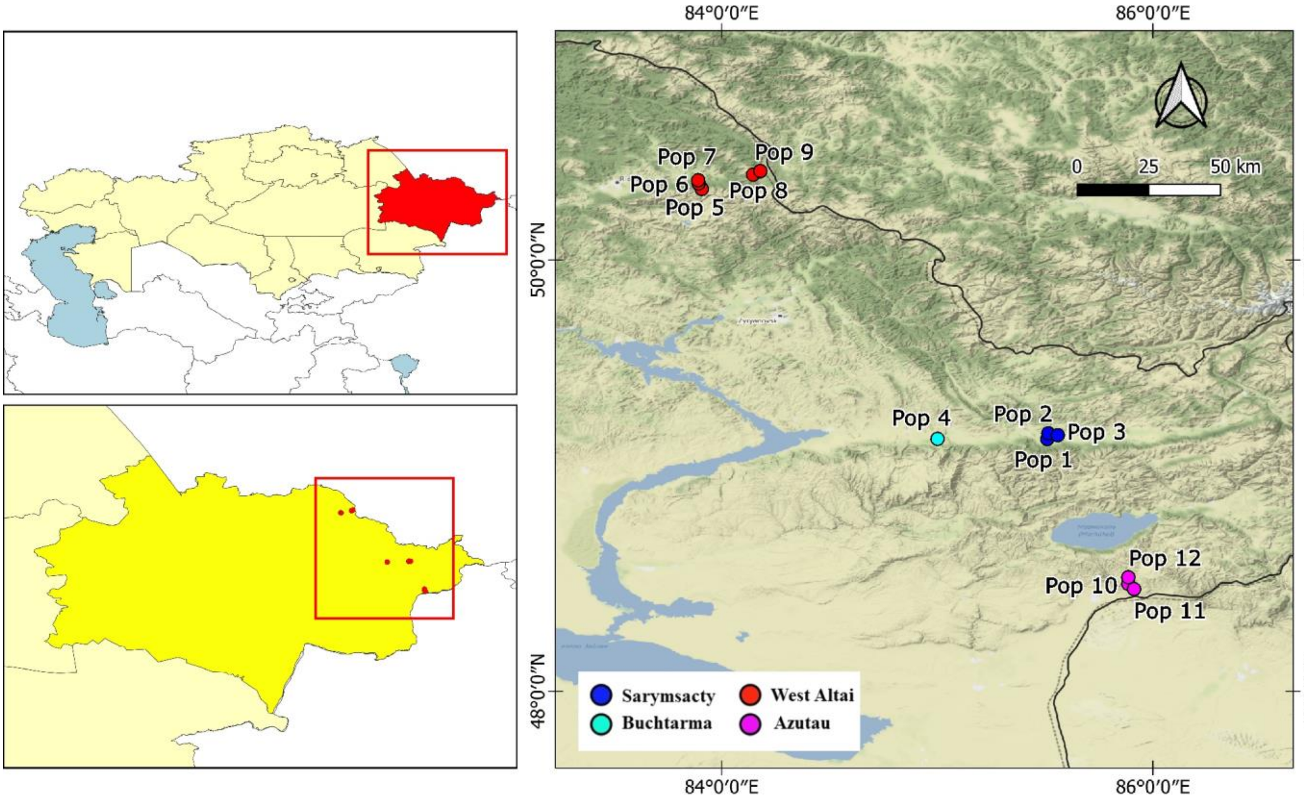


Figure 1. *Dactylorhiza fuchsii* populations in the Kazakhstan Altai

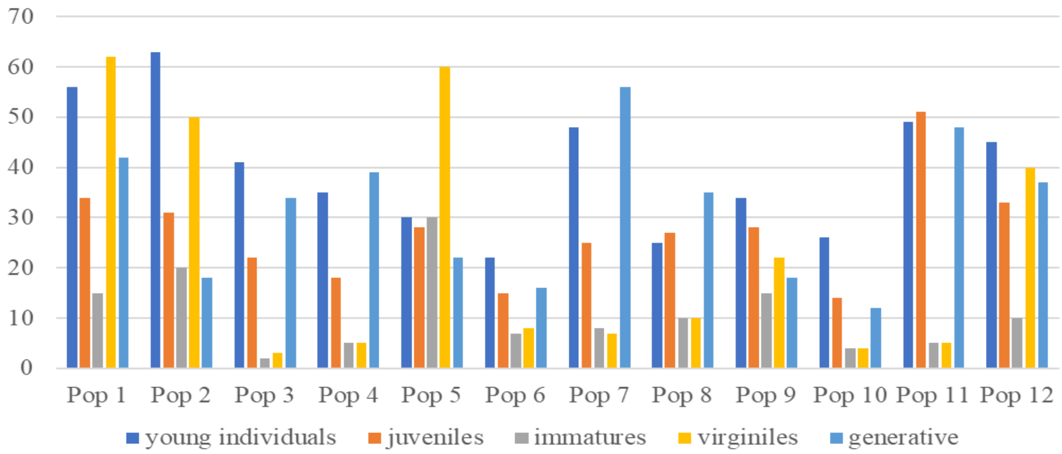


Figure 2. Self-renewal of populations: X axis - growth stages for populations of *Dactylorhiza fuchsii*; Y axis - individuals, total

Table 1. Characteristics of localities of *Dactylorhiza fuchsii* populations

No. Pop, main dominants in plant community	Location	Geographical coordinates	*S	**L	**F	**R	**N	Habitat
Sarymsacty region								
Pop 1 (*Calamagrostis epigeios* (L.) Roth, *Thalictrum simplex* L., *Rubus saxatilis* L.)	The southeastern foothills of the Bukhtarma Mountains, 3 km southwest of the village Katon-Karagai	49.18361 N 85.51472 E 912 m a.s.l.	500	4	3	4	4	Wet meadows, glades, heavily sparse birch forest
Pop 2 (*Filipendula ulmaria* (L.) Maxim, *Sonchus arvensis* L., *Equisetum arvense* L.)	North-western foothills of the Sarymsakty ridge, in the vicinity of the village Topkain	49.19055 N 85.51777 E 857 m a.s.l.	350	3	3-4	4	4	Under the canopy of a birch forest, in a stream valley as part of shrub formations
Pop 3 (*Empetrum nigrum* L., *Vaccinium vitis-idaea* L.)	Sarymsakty ridge, neighborhood village Katon-Karagai	49.18833 N 85.55833 E 946 m a.s.l.	250	2-3	4	3	3	Swampy forest edges
Buchtarma region								
Pop 4 (*Tussilago farfara* L., *Equisetum sylvaticum* L.)	The western part of the Bukhtarma Mountains, in the vicinity of the village Maimyr, in the valley of the Naryn River, the Botash tract	49.17055 N 85.00027 E 739 m a.s.l.	100	3	3-4	3	4	Under the canopy of the tree layer, a narrow strip along the stream
West Altai region								
Pop 5 (*Allium microdictyon* Prokh., *Dactylis glomerata* L., *Phleum phleoides*)	Southwestern foothills of the Ivanov Range	50.34388 N 83.89277 E 1212 m a.s.l.	550	3	3	2-3	3	on wet moss glades with diffused lighting
Pop 6 (*Carex elongata* L., *Equisetum arvense* L.)	South-western foothills of the Ivanov Range, in the valley of the river Bolshaya Poperechka, the vicinity of the village Sery Lug.	50.34888 N 83.89194 E 1197 m a.s.l.	150	4	4-5	3	3	Wetland in the bed of a mountain stream
Pop 7 (*Equisetum arvense* L., *Festuca altissima* All., *Agrostis gigantea* Roth)	Northern slopes of the Ivanov ridge, in the vicinity of the village Sery Lug	50.34916 N 83.89194 E 1184 m a.s.l.	100	4	4	3	3	Valley of a mountain stream, steep coastal slopes, steepness 45-60º
Pop 8 (*Carex elongata* L., *Juncus compressus* Jacq., *Spirea media* Franz Schmidt)	Southwestern slopes of the Lineysky ridge, Krutma tract	50.3975 N 84.14833 E 1359 m a.s.l.	200	4-5	3	3	3	Wet meadow. The species is settled in a narrow strip along the stream bed
Pop 9 (*Betula verucosa* Ehrh., *B. microphylla* Bunge, *Carex elongata* L.)	Western spurs of the Lineysky ridge, in the valley of the Black Uba river.	50.41388 N 84.18055 E 1300 m a.s.l.	250	3	4	3-4	3	Edge of shrub and tree communities
Azutau region								
Pop 10 (*Calamagrostis epigeois* (L.) Roth, *Prunella vulgaris* L.)	North-western slopes of the Azutau ridge	48.50194 N 85.88666 E 1365 m a.s.l.	100	4	3	3-4	3	A depression overgrown with *Salix viminalis* L.
Pop 11 (*Salix caprea* L., *S. viminalis* L., *Equisetum sylvaticum* L., *Carex disticha* Huds.)	Southern Altai, Azutau ridge, Mramorny pass, northwestern slope	48.47111 N 85.91166 E 1370 m a.s.l.	200	3	3	3-4	3	Willow thickets from *Salix caprea* L. and *Salix viminalis* L.
Pop 12 (*Carex juncella* Fries)	North-eastern foothills of the Azutau ridge. Tract Karagashty	48.522778 N 85.89027 E 1290 m a.s.l.	500	4	4	3	2-3	Meadow depression, oriented from southwest to northeast

Note: Pop: populations; *S: area, m ^{2}. **Note on the designation of the levels of ecological scales (Landolt 1977): L: illuminance scale: 1: completely shady plant, often growing in conditions less than 3% of full light; 2: mostly shady plant (more often at 10% of full illumination); 3: penumbra plant (at a relative illumination of more than 10%); 4: semi-light (often in full light, but sometimes with some shading); 5: completely light plant, unable to tolerate shading. F: humidity scale: 1: on very dry soils, indicator of dry habitats; 2: on dry soils, avoids very dry and very wet soils; 3: on medium dry to moist soils; 4: on wet to damp soils; 5: on soils saturated with water, avoids moderately moist habitats; 5w: on very damp soils after rain; 5u: in flooded areas; 5s: plants with leaves floating in the water; 5i: plants live in water, but most of their leaves are above water. R: soil acidity scale: 1: on very acidic soils (pH less than 4.5); 2: on acidic soils (pH 3.5-5.6); 3: on slightly acidic soils (pH 4,5-7,5), never on very acidic, but sometimes on neutral and slightly alkaline soils; 4: on alkaline soils (pH 5.5-8.0); 5: only on alkaline soils (pH above 6.5); x: on very acidic and alkaline soils, often avoids medium conditions, as it does not withstand competition with other species. N: soil nutrient richness scale (especially nitrogen): 1: on very rich soils; 2: on poor soils; 3: on soils from medium-dry to medium-rich; 4: on rich soil; 5: on soil rich (especially in nitrogen), never found on poor.

Table 2. Species diversity of accompanying species for *Dactylorhiza fuchsii* regions

Region	Number of species	Herbaceous species	Tree and shrub species	mesophytes	mesohygrophytes	mesoxerophytes
Sarymsacty	112	92 (82%)	20 (18%)	77 (68%)	22 (20%)	13 (12%)
Buchtarma	59	49 (83%)	10 (17%)	43 (73%)	11 (19%)	5 (8%)
West Altai	141	125 (89%)	16 (11%)	102 (72%)	26 (19%)	13 (9%)
Azutau	77	74 (96%)	3 (4%)	56 (73%)	14 (18%)	7 (9%)
Total	251	219 (87.5%)	32 (12.5%)	179(71.5%)	48 (19%)	24 (9.5%)

Table 3. Floral composition similarity of *Dactylorhiza fuchsii* regions based on the Jaccard coefficient

Jaccard coefficient	Sarymsacty	Buchtarma	West Altai
Buchtarma	24%		
West Altai	23%	12%	
Azutau	23%	21%	17%

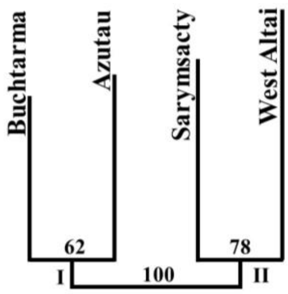


Figure 3. Dendrogram by species similarity of *Dactylorhiza fuchsii* regions

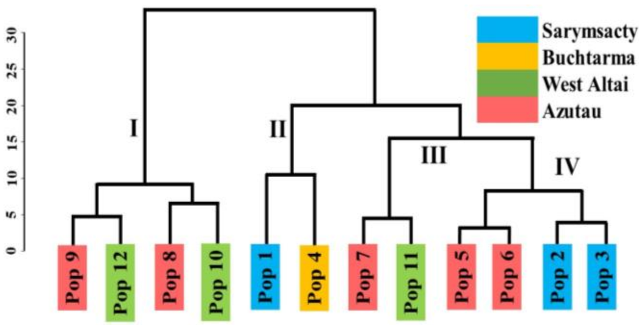


Figure 4. Cluster analysis of the similarity of *Dactylorhiza fuchsii* populations by 10 external morphometric features

Principal component analysis (PCA) by regions difference (Figure 5) showed the similarities and differences of populations within each region. Some isolation of Sarymsacty and Buchtarma from other regions was revealed. West Altai and Azutau have overlapping ellipses for Pop 7 and Pop 12, and are morphometrically similar. Apparently, this was influenced by similar altitudinal zoning, according to which these regions are quite close (1100-1300 m a.s.l.) (Table 1). Thus, the PCA data confirms the previously presented cluster analysis.

Principal component analysis (PCA) by population difference (Figure 6) demonstrates the differences and similarities of all samples of the studied populations. Significant isolation of samples of Pop 1 related to Sarymsacty and Pop 4 related to Buchtarma along coordinate 1 from other individuals was revealed. The Buchtarma and Azutau samples were located diffusely in one group, which confirms the uniformity of the external morphometry of individuals in these populations. The quality of the sample of individuals for analysis is high, as evidenced by the qualitative grouping of populations.

Correlation analysis of the dependence of the morphometric characteristics of generative individuals on environmental conditions using the Pearson coefficient (Figure 7.A) showed a stable direct correlation between the length of basal leaves and the number of flowers in the inflorescence and the length of the inflorescence (0.95). Moreover, the width of the basal leaves has a stable inverse correlation to the number of flowers (-0.52) and the length of the inflorescence (-0.38). This feature can be practically used for the selection of developed plants after the end of the growing season in the absence of flowering individuals. The scale of illumination and humidity did not show stable correlations with morphometric features. The scale of soil acidity has a direct correlation with the number of flowers: with a decrease in acidity, the flowering of generative individuals noticeably increases (0.51). The soil nutrient richness scale shows a direct correlation with the height of individuals (0.61), which contradicts the generally accepted notion that *D. fuchsii* prefers poor soils. The study of the relationships between the total number, density and ecological conditions of *D. fuchsii* habitats (Figure 7.B) showed insignificant positive correlations between the density of generative individuals and illumination (0,54), as well as the total number of vegetative individuals and soil nutrient richness (0,55).

ANOVA revealed a significant effect of four environmental factors on the morphological traits of *D. fuchsii* generative individuals. Among studied environmental factors, soil nutrient richness (N) and humidity (F) had demonstrated the broadest significant effects (P-values from < 2e-16 to 0.001 for N and from 8.02e-09 to 0.02 for F) on plants morphology influencing eight out of ten morphological traits except SLW and BLW for N and PH and PL for F (Table 5).

Table 4. Results of measuring morphometric characteristics

Feature name		Pop 1	Pop 2	Pop 3	Pop 4	Pop 5	Pop 6	Pop 7	Pop 8	Pop 9	Pop 10	Pop 11	Pop 12
PH (Plant height)	(M±m)	50.800±2.981	43.450±2.566	42.300±3.025	43.450±3.022	36.650±0.417	38.700±2.877	35.800±1.759	21.800±2.093	30.650±1.206	25.100±2.396	36.000±1.203	28.350±2.001
	min-max	35-61	31-53	36-56	33-56	32-43	29-52	29-43	14-30	27-35	21-34	32-40	24-35
	C%	12. 55	12.63	15.30	14.88	14.11	15.90	10.51	20.54	8.42	20.43	7.15	15.10
	P%	2.80	2.82	3.42	3.32	3.15	3.55	2.35	4.59	1.88	4.56	1.59	3.37
NL (Number of leaves)	(M±m)	5.950±0.385	6.750±0.397	4.850±0.348	6.750±0.397	4.850±0.348	4.400±0. 234	4.550±0.238	3.950±0.385	4.350±0.228	5.450±0.441	6.450±0.238	5.600±0.234
	min-max	5-7	5-8	4-6	5-8	4-6	4-5	4-5	3-5	4-5	4-7	6-7	5-6
	C%	13.87	12.60	15. 36	12.60	15.36	11.42	11.21	20.90	11.24	17.33	7.91	8.97
	P%	3.10	2.81	3.43	2.81	3.43	2.55	2.50	4.67	2.51	3.87	1.76	2.00
IL (Inflorescence length)	(M±m)	9.700±0.774	3.550±0.272	4.700±0.342	6.055±0.427	3.650±0.322	4.550±0. 441	4.050±0.261	3.550±0.184	3.900±0.368	4.700±0.342	5.950±0.490	2.950±0.354
	min-max	6-13	2.5-4	4-6	5-8	2.5-4.5	3-6	3.5-5	3-4	3-5	4-6	4-7	2-4
	C%	17. 08	16.41	15.58	15.12	18.90	20.75	13.81	11.09	20.20	15.58	17.64	25.73
	P%	3.82	3.66	3.48	3.38	4.22	4.64	3.08	2.48	4.51	3.48	3.94	5.75
IW (Inflorescence diametr)	(M±m)	2.800±0.171	1.780±0.153	1.960±0.162	2.600±0.194	1.675±0.137	2.425±0.204	2.100±0.279	1.850±0.153	1.915±0.187	2.450±0.181	2.400±0.236	1.415±0.190
	min-max	2.6 - 3	1.5-2	1.5-2.5	2-3	1-2	2-3	1.5-3	1.5-2.5	1.5-2.5	2-3.2	1.5-3	1-2
	C%	13. 10	18.46	17.78	16.02	17.52	18.04	28.48	17.75	20.97	15.80	21.11	28.75
	P%	2.93	4.12	3.97	3.58	3.91	4.03	6.37	3. 97	4.69	3.53	4.72	6.42
PL (Peduncle length)	(M±m)	7. 950±0.686	7.750±0.522	5.100±0.258	5.530±0.832	5.300±0. 396	7.150±1.085	4.950±0.354	5.100±0.258	4.300±0.307	3.450±0.213	5.900±0.623	3.100±0.398
	min-max	5-11	5-9	4-6	2.5-8.5	4-7	5-12	4-6	4-6	3.5-5	3-4	4-8	2-4
	C%	18.46	14.42	10.8	32.19	16.02	32.49	15.33	10.83	15.27	13.21	22.60	27.49
	P%	4.12	3.22	2.42	7.2	3.58	7.26	3.42	2.42	3.41	2.95	5.05	6.14
NFI (Number of flowers per inflorescence)	(M±m)	22.250±0.856	8.400±0.684	9.650±0.715	28.100±2.728	11.900±1.646	12.200±0. 671	21.000±3.308	9.100±0.842	9.700±0.728	12.300±1.954	19.700±2.754	8.850±0.762
	min-max	19-26	7-12	8-12	20-37	8-18	10-14	11-40	7-12	8-12	7-18	7-30	7-12
	C%	8.23	17.44	15.86	20.77	29.60	11.77	33.70	19.81	16.07	33.99	29.92	18.43
	P%	1.84	3.90	3.54	4.64	6.61	2.63	7.53	4.43	3.59	7.60	6.69	4.12
SLL (Stem leaf length)	(M±m)	9.840±0.602	9.800±0.559	9.500±0.479	10.250±0.782	9.000±0.428	8.950±0. 633	6.875±0.311	6.375±0.407	9.000±0.877	10.250±0.782	8.800±0.865	6.250±0.334
	min-max	8-12.3	8-12	8-11.5	8-12.5	7.5-10.5	7-11	6-8	5-7.5	6-12	8-14	6-12	5-7
	C%	13. 09	12.20	10.79	16.33	10.19	15.15	9.69	13.67	20.86	16.33	21.05	11.46
	P%	2.92	2.73	2.41	3.65	2.27	3.38	2.16	3.05	4.66	3.65	4.70	2.56
SLW (Stem leaf width)	(M±m)	1.955±0.187	1.975±0.239	1.905±0.154	1.850±0.274	1.575±0.189	1.250±0. 119	1.050±0.159	1.900±0.114	1.875±0.144	1.875±0.149	1.625±0.225	1.800±0.206
	min-max	1-2.5	1-3	1-2.3	1-3	1-2	1-1.5	0.5-1.5	1.5-2.5	1.5-2.5	1.5-2.5	1-2	1-2.5
	C%	20.55	25.91	17.32	31.73	25.80	20.51	32.48	12.89	16.49	17.03	29.73	24.51
	P%	4.59	5.79	3.87	7.09	5.76	4.58	7.26	2.88	3.68	3.80	6.65	5.48
BLL (Basal leaf length)	(M±m)	10.690±0.823	7.550±0.490	7.450±0.772	8.715±0.702	8.825±0.759	7.750±0.740	6.925±0.622	6.775±0.298	6.900±0.335	6.775±0.298	9.000±0.448	8.450±0.669
	min-max	8-13.5	5-9	6-12	6.8-11	7-12	5-9	4.5-9	6-8	6-8	6-8	7.5-10	6-11
	C%	16.48	13.90	22.19	17.25	18.40	20.45	19.23	9.41	10.40	9.41	10.66	16.94
	P%	3.68	3.10	4.96	3.85	4.11	4.57	4.30	2.10	2.32	2.10	2.38	3.78
BLW (Basal leaf width)	(M±m)	3.770±0.331	2.395±0.173	2.700±0.358	3.375±0.225	2.850±0.313	2.550±0.292	2.385±0.290	1.825±0.156	2.350±0.274	2.675±0.265	3.620±0.240	3.412±0.142
	min-max	3-5	2-3	1.5-4	3-4	2-4	1.5-3	1-3	1.5-2.5	1.5-3	1.5-3.5	3-4.5	2.5-4
	C%	17.08	15.47	28.41	14.31	23.53	24.55	26.03	18.37	24.98	21.24	14.24	13.56
	P%	3.82	3.46	6.35	3.20	5.26	5.49	5.82	4.10	5.58	4.75	3.18	2.75

Note: M - the average value of the morphometric feature, m - allowable limits, min-max - minimum and maximum feature values, C% - coefficient of variation of a feature, P% - the standart error of the sample mean (accuracy of the experiment).

Slightly less broad, but still significant effect (P-values ranged from 2.78e-10 to 0.0005) was observed for soil acidity (R) affecting seven out of ten morphological traits. Finally, illuminance (L) showed the smallest impact on plants morphology influencing only PH, NL, SLL, and SLW (P-values ranged from 3.67e-14 to 0.02). The list of morphological traits with significant environmental effects of all four factors included NL (P-values from 5.73e-10 to 2.15e-05) and SLL (P-values from 5.61e-12 to 0.002) (Table 5).

Characteristics of vitality structure of *D. fuchsii* populations are presented in Table 6. When assessing the vitality type of the population using the Q criterion, it was found that majority of *D. fuchsii* populations are characterized as depressive. Progressive populations are Pop 1, Pop 2 and Pop 8. In these populations, the proportion of individuals of the progressive class ranges from 24 to 47%, and the proportion of individuals of the lower class is from 23 to 32%. Pop 4, which represents Buchtarma region, is the only equilibrium. Among the depressive populations, the lowest vitality (0.806 and 0.766) and Iq (0.61 and 0.38) indices are characterized by Pop 9 and Pop 10, the highest by Pop 7 and Pop 11, where the Iq indices were 0.92 and 0.85 respectively.

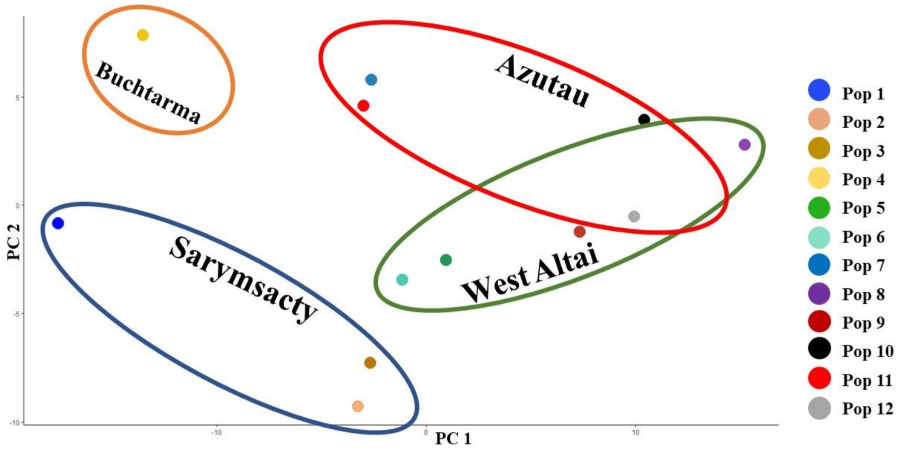


Figure 5. PCA for *Dactylorhiza fuchsii* population difference based on external morphometrics

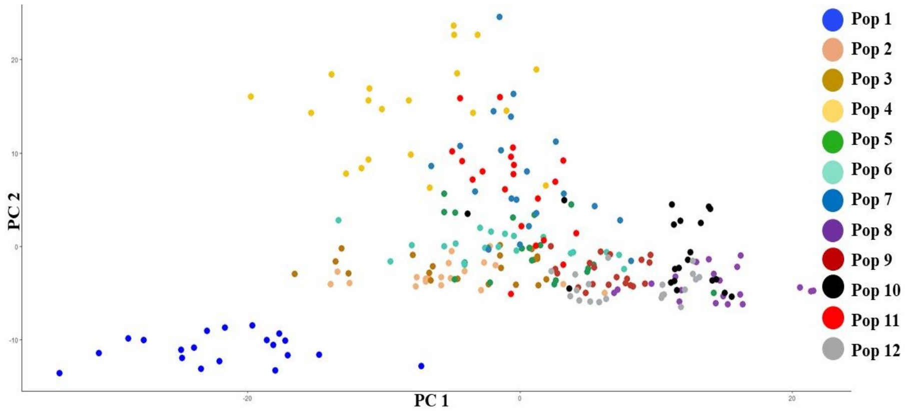


Figure 6. PCA by population difference based on morphometric characteristics

Table 5. ANOVA of morphological traits influenced by environmental factors

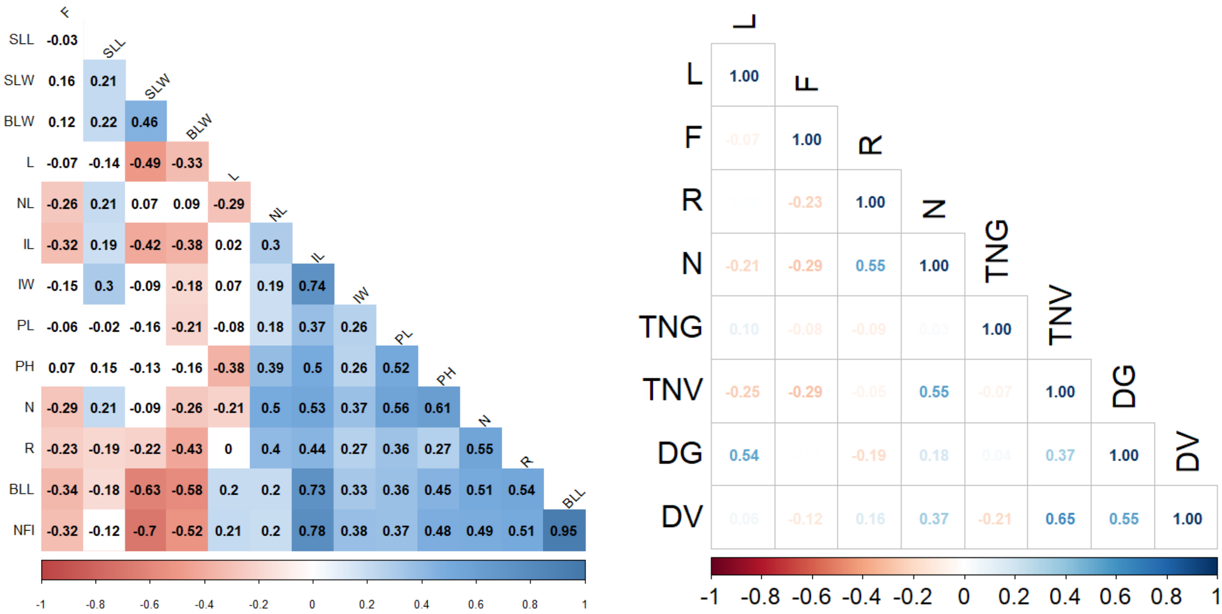
Trait/ Factor	L	F	R	N
PH	3.67e-14***	0.35ns	1.63e-09***	< 2e-16***
NL	1.05e-07***	2.33e-07***	5.73e-10***	2.15e-05***
IL	0.72ns	8.02e-09***	2.07e-11***	2.95e-09***
IW	0.23ns	0.02*	8.33e-05***	4.77e-06***
PL	0.14ns	0.22ns	2.78e-10***	5.96e-15***
NFI	0.70ns	0.002**	0.74ns	4.32e-15***
SLL	5.61e-12***	0.002**	1.67e-06***	2.10e-05***
SLW	0.02*	2.09e-05***	0.0005***	0.92ns
BLL	0.26ns	0.0002***	0.17ns	0.001**
BLW	0.08ns	0.02*	0.14ns	0.72ns

Note: ns: not significant; *: P < 0.05; **: P < 0.01; ***: P < 0.001

Table 6. Dynamics of the vitality structure of *Dactylorhiza fuchsii* populations

Pop	The proportion of individuals by classes of vitality, %			Q	I_q	Vital type of population	Population vitality index, IVC
	a	b	c				
1	27	50	23	38.5	1.67	Progressive	1.409
2	47	29	24	38	1.58	Progressive	1.066
3	22	37	41	29.5	0.72	Depressive	1.001
4	36	31	33	33.5	1.01	Equilibrium	1.335
5	25	37	38	31	0.81	Depressive	0.974
6	33	29	38	31	0.81	Depressive	1.013
7	28	37	35	32.5	0.92	Depressive	1.056
8	24	44	32	34	1.06	Progressive	0.674
9	34	21	45	27.5	0.61	Depressive	0.806
10	23	20	57	21.5	0.38	Depressive	0.766
11	36	27	37	31.5	0.85	Depressive	1.112
12	36	22	42	29	0.71	Depressive	0.784

Note: a: high vitality, b: medium, c: low; Q = (a+b)/2; I_q = (a+b)/2c; IVC: vitality coefficient. IVC=$\frac{\sum_{i=1}^{N} x_i/\bar{x}}{N}$, x_i: average value of the i-th feature in the population; $\bar{x}$: average value of the i-th feature for all populations; N: number of features. Q>c: progressive, Q=c: equilibrium, Q<c: depressive



A B

Figure 7. A. Correlation coefficients (r) between metric features of *Dactylorhiza fuchsii* and conditions of the external ecological environment according to Pearson; B. Correlation coefficients (r) between population characteristics of communities and environmental conditions. Correlations with significance P < 0.05 are highlighted in color. Red color is for negative and blue color is for positive correlations. Colors intensity demonstrates the strength of correlation according to the scale given. Note: L: illuminance scale; F: humidity scale; R: soil acidity scale; N: soil nutrient richness scale; PH: Plant height; NL: Number of leaves; IL: Inflorescence length; IW: Inflorescence diamdiameter: Peduncle length; SLL: Stem leaf length; SLW: Stem leaf width; BLL: Basal leaf length; BLW: Basal leaf width; NFI: Number of flowers per inflorescence; TNG: total number of generative individuals; TNV: total number of vegetative individuals; DG: density of generative individuals; DV: density of vegetative individuals.

To establish the Spearman rank correlation coefficient (Table 7) in floristic composition for the studied populations, a correlation analysis of the spectrum for 10 leading families of accompanying species in floristic composition of each population to the flora of the related *D. fuchsii* regions, to the flora of accompanying species for the studied *D. fuchsii* populations and to the flora of Kazakhstan Altai (KAM) was carried out.

The correlation between the leading families of accompanying species for populations and the related regions is usually strong and direct (0.602-0.957), less often weak and direct (0.432). It was found that Pop 4 and Buchtarma region have the maximum similarity (0.957) and direct ratio.

Table 7. Spearman's rank correlation coefficient in floristic composition of the studied populations

No. populations	**Pop 1**	**Pop 2**	**Pop 3**	**Pop 4**	**Pop 5**	**Pop 6**	**Pop 7**	**Pop 8**	**Pop 9**	**Pop 10**	**Pop 11**	**Pop 12**	**Sarymsacty**	**Buchtarma**	**West Altai**	**Azutau**	**Flora of accompanying species for the *D. fuchsii* populations**	**Flora of KAM***
Sarymsacty	0.849	0.746	0.432	-	-	-	-	-	-	-	-	-		0.644	0.545	0.655	0.635	0.473
Buchtarma	-	-	-	0.957	-	-	-	-	-	-	-	-	0.644	-	0.504	0.656	0.806	0.553
West Altai	-	-	-	-	0.724	0.635	0.602	0.836	0.683	-	-	-	0.545	0.504	-	0.241	0.888	0.702
Azutau	-	-	-	-	-	-	-	-	-	0.773	0.899	0.897	0.655	0.656	0.241	-	0.516	0.197
Flora of accompanying species for the *D. fuchsii* populations	0.308	0.286	0.0444	0.754	0.444	0.728	0.494	0.932	0.585	0.428	0.367	0.492	0.635	0.806	0.888	0.516	-	0.743
Flora of KAM*	0.31	0.24	0.204	0.525	0.531	0.427	0.642	0.753	0.381	0.418	0.0601	0.27	0.473	0.553	0.702	0.197	0.743	-

Note: KAM: Flora of Kazakhstan Altai mountains; * value of Spearman's rank correlation coefficient ($p<0.05$)

Table 8. Leading flora families of *Dactylorhiza fuchsii* regions by number of species

Family	Flora of *D. fuchsii* regions		Flora of Kazakhstan Altai
	Number of species. % of the total number	Number of genera. % of the total number	Number of species, % of the total number
Poaceae Barnhart	33/13.15	19/12.34	308/12.6
Rosaceae Juss.	24/9.56	15/9.74	109/4.5
Ranunculaceae Juss.	20/7.97	8/5.19	103/4.2
Asteraceae Dumort.	19/7.57	16/10.39	324/13.3
Cyperaceae Juss.	15/5.97	3/1.93	96/3.9
Lamiaceae Martinov	10/3.98	7/4.55	77/3.2
Fabaceae Lindl.	10/3.98	7/4.55	183/7.5
Apiaceae Lindl.	10/3.98	8/5.19	71/2.9
Orchidaceae Juss.	9/2.79	7/4.55	22/0.9
Caryophyllaceae Juss.	8/3.19	6/3.91	81/3.3
Total	150/59.76	97/62.99	1256/51.8

Spearman's rank correlation for regions shows the difference between individual elements due to the specifics of local floras. The maximum similarity is observed between West Altai and flora of accompanying species for *D. fuchsii* populations (0.888), which is explained by the high correspondence of the species composition of this region to the ecological optimum of the species. A low correlation can be traced in Azutau to KAM, since this population is incomplete and is represented by a limited number of families. When comparing the floristic composition of *D. fuchsii* regions with the flora of Kazakhstan Altai (Table 8), it was found that the families Asteraceae Dumort., Fabaceae Lindl., Ranunculaceae Juss., Rosaceae Juss. significantly differ in the share of participation in the formation of the floristic composition. This is due to the low number of xeromesophytic species and the predominant number of mesophytic species, which are typical for mixed and dark coniferous forests.

Discussion

Previously, Bateman and Denholm (1989) conducted a study of 52 morphological characteristics in 20 *D. fuchsii* populations in Britain and Ireland. Dufrêne et al (1991) conducted a biostatistical study of 12 *D. fuchsii* populations based on 28 morphometric traits for Western Europe. Taraška et al. (2021) conducted a comparative analysis of *D. fuchsii* populations based on 24 morphological characters for 27 sites from Central Europe: Austria, Czech Republic, Germany, Hungary, Poland, Romania, Slovakia, and Slovenia. Kirillova and Kirillov (2013) conducted a population study of 28 *D. fuchsii* populations based on 19 morphometric characters in the European part of Russia.

We also conducted a study of 12 populations according to 10 morphometric characters for the Kazakhstan part of the Altai mountains. Thus, the results of this study harmoniously complement the fundamental study on the state of *D. fuchsii* populations throughout the distribution range of the species. Additional attention was paid to the floristic composition of these communities, as one of the main factors of the ecological optimum of the species in the study area.

The study of flora and population plasticity by the Jaccard coefficient showed a high heterogeneity of the studied populations, which indicates the selectivity and significance of associated species for the state of *D. fuchsii*. The cluster dendrogram showed a clear dependence of the floristic composition of populations on geographical location in terms of species similarity and difference of communities. West Altai is situated in the western part of the Kazakhstan Altai, is located in isolation from Sarymsacty, Buchtarma and Azutau, which belong to the southern part of the Kazakhstan Altai. It can be assumed that the flora of West Altai regions has more Siberian species in its structure, in contrast to other *D. fuchsii* regions, which are characterized by a large number of Central Asian species.

The study of external morphometry and geographic location of populations did not reveal a clear relationship. PCA analysis shows that the external structure is more influenced by vertical zoning, rather than geographical separation. Thus, Sarymsacty and Buchtarma regions, which grow at an altitude of 700-900 m.a.s.l., are very similar, while those located at an altitude of 1100-1300 m.a.s.l. West Altai and Azutau regions have a stable similarity as alpine populations.

In addition, Pearson's correlation analysis of floristic composition showed a stable direct and inverse dependence of the morphometric characteristics of *D. fuchsii* on some environmental conditions, such as soil acidity and soil nutrient richness. A direct correlation between the density of generative individuals and the illumination of habitats is logically explained by the dependence of the flowering process on the exposure, and the richness of the substrate determines the germination of young individuals. ANOVA analysis of variance fully confirmed the previously obtained results of Pearson's correlation analysis. The light factor has a limited effect on the morphometric characteristics of the plant, and soil acidity and nutrient richness has a wide range of influence. Paradoxically, there is no effect of humidity on plant height. It can be assumed that *D. fuchsii*, being a forest mesophyte, unlike other species of the genus, has a high amplitude of variation.

Dactylorhiza fuchsii regions have low vitality, and most populations are characterized as depressive. At the same time, progressive Pop 1, Pop 2 and Pop 8 have high rates of self-renewal with a sufficient number of young vegetative individuals. Depressive Pop 9 and Pop 10 have average self-renewal rates, but are the smallest in terms of the number of generative individuals (Figure 2).

Rank analysis of the leading families in floristic composition according to the Spearman coefficient showed the incompleteness of the flora of *D. fuchsii* populations in the Kazakhstan Altai. Correlations are usually direct and strong. The similarity of populations to the flora of the Kazakhstan Altai is noticeably reduced, which is explained by the xerophytization of the flora of the Kazakhstan Altai and the large number of mesophytic and hygromesophytic species in *D. fuchsii* populations. The lowest indicators are Pop 11 and Pop 12, geographically related to the Mramorny Pass, which is a local biodiversity locus in the Kazakhstan Altai and Central Asia as a whole.

The presence of weed species in communities (Table S1): *Heracleum dissectum* Ledeb., *Artemisia vulgaris* L., *Cirsium incanum* (S.G. Gmel.) Fisch., *Sonchus arvensis* L. confirms the presence of anthropogenic pressure on the studied populations. According to the ratio of vascular spores, gymnosperms and angiosperms (Table S1), the flora of *D. fuchsii* populations reflects the general patterns inherent in the floras of the ridges of the Altai Mountains. A low percentage of species and genera belonging to the main ten families in floristic composition, 59.76%, indicates a low degree of anthropogenic pressure and flora transformation, which is relatively consistent with the general indicators of the Kazakhstan Altai, 51.8%. It has been established that in terms of morphometric parameters, floristic composition and environmental conditions, the optimum of *D. fuchsii* falls on *Calamagrostis-Thalictrum simplex-Rubus saxatilis, Filipendula ulmaria-Sonchus arvensis-Equisetum arvense, Allium microdictyon-Dactylis glomerata-Phleum phleoides, Equisetum arvense-Festuca altissima-Agrostis gigantea, Betula verucosa-B. microphylla-Carex elongata* plant communities, which occupy the edges of mixed and dark coniferous forests, are found under the canopy of high shrubs, as well as along the valleys of mountain streams on moss litter.

In conclusion when studying the current state of *Dactylorhiza fuchsii* populations in the Kazakhstan Altai, 12 populations of an endangered species were found. As a result of the analysis, it was found that all the studied populations differ markedly in floristic composition, phytocenotic affiliation and ecological confinement. Indicators of vitality and vitality structure indicate that the populations are noticeably weakened, in the majority they are depressive.

The flora of accompanying species of *D. fuchsii* populations is incomplete; a high difference in individual elements has been established, due to the specifics of the local flora, as well as the uniqueness of regional loci. It was found that the morphometric dimensions of generative individuals within the Kazakhstan Altai are significantly affected by altitudinal zoning, and not geographical fragmentation. Geographic affiliation significantly affects the floristic composition of communities with *D. fuchsii*. Species complexes of the western part of the Kazakhstan Altai are qualitatively different from those of the southern part. A noticeable effect on the morphometric characteristics of *D. fuchsii* was found to be environmental conditions, in particular soil acidity and soil nutrient richness. The flora of accompanying species of *D. fuchsii* populations is significantly comparable with the flora of the entire Kazakhstan Altai. But it differs in the share of participation of some families in the formation of the floristic composition. This is due to the low number of xeromesophytic species and the predominant number of mesophytic species characteristic of mixed and dark coniferous forests.

The ecological optimum of the species falls on Calamagrostis-Thalictrum simplex-Rubus saxatilis, Filipendula ulmaria-Sonchus arvensis-Equisetum arvense, Allium microdictyon-Dactylis glomerata-Phleum phleoides, Equisetum arvense-Festuca altissima-Agrostis gigantea, Betula verucosa-B. microphylla-Carex elongata plant communities, which occupy the edges of mixed and dark coniferous forests, are found under the canopy of high shrubs, as well as along the valleys of mountain streams on moss litter. All studied populations require additional conservation and protection measures. The data obtained as a result of the study can serve as a basis for the development of measures for the conservation and protection of *D. fuchsii* populations in the Kazakhstan Altai.

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REFERENCES

Aybeke M, Sezik E, Olgun G. 2010. Vegetative anatomy of some *Ophrys*, *Orchis* and *Dactylorhiza* (Orchidaceae) taxa in Trakya region of Turkey. Flora 205: 73-89

Bajtulin IO, Kotukhov Ju A. 2011. Flora sosudistyh rastenij Kazahstanskogo Altaja [Flora of vascular plants of Kazakhstan Altai], Almaty [in Russian].

Bateman RM, Denholm I. 1989. A reappraisal of the British and Irish dactylorchids, 3. The spotted-orchids. Watsonia 17: 319-349.

Box MS., Dodsworth S., Rudall PJ., Bateman RM., Glover BJ. 2012. Flower-specific KNOX phenotype in the orchid *Dactylorhiza* fuchsii. J. Exp. Bot 63 (13): 4811-4819. DOI: 10.1093/jxb/ers152

Danilova AN, Sumbembayev AA. 2021 The status of the *Dactylorhiza incarnata* populations in the Kalba Altai, Kazakhstan. Biodiversitas. 22 (8): 3180-3195. DOI: 10.13057/biodiv/d220812

De Hert K, Jacquemyn H, Van Glabeke S, Roldan-Ruiz I, Vandepitte K, Leus L, Honnay O. 2012. Reproductive isolation and hybridization in sympatric populations of three *Dactylorhiza* species (Orchidaceae) with different ploidy levels. Annals of Botany 109 (4): 709-720. DOI: 10.1093/aob/mcr305

Đorđević V, Jovanović S, Stevanović V. 2014. *Dactylorhiza* fuchsii (Orchidaceae), a new species in the flora of Serbia. Arch Biol Sci 66 (3): 1227-1232. DOI:10.2298/ABS1403227D

Dufrêne M, Gathoye JL, Tyteca D. 1991. Biostatistical studies on western European *Dactylorhiza* (Orchidaceae)-the D. maculata group. Plant Syst Evol 175 (1): 55-72.

Efimov PG, Philippov EG, Krivenko DA. 2016. Allopolyploid speciation in Siberian *Dactylorhiza* (Orchidaceae, Orchidoideae). Phytotaxa 258 (2): 101-120. DOI: 10.11646/phytotaxa.258.2.1

Egorova Nyu, Suleimanova VN. 2021. Variability of morphological structures in *Cypripedium calceolus* (Orchidaceae) and their relationship with the habitat conditions in the southern taiga ecosystems, Russia Nat Conserv Res 6 (1): 28-41. DOI: 10.24189/ncr.2021.006

Gutowski JM. 1990. Pollination of the orchid *Dactylorhiza fuchsii* by longhorn beetles in primeval forests of Northeastern Poland. Biol Conserv 51 (4): 287-297. DOI: 10.1016/0006-3207(90)90114-5

Ishbirdin AR, Ishmuratova MM. 2004 Adaptive morphogenesis and ecological-coenotic strategies for the survival of herbaceous plants. Methods of population biology. Collection of materials VII All-Russian. Population Seminar (Syktyvkar, February 16-21, 2004). Syktyvkar, 2: 113-120.

IUCN. 2020. The IUCN Red List of Threatened Species. (http://www.iucnredlist.org).

Jacquemyn H, Deja A, De hert K, Cachapa Bailarote B, Lievens B. 2012. Variation in Mycorrhizal Associations with Tulasnelloid Fungi among Populations of Five *Dactylorhiza* Species. PLoS ONE 7(8): e42212. DOI: 10.1371/journal.pone.0042212

Jakobsone G. 2008. Morphogenesis of wild orchid *Dactylorhiza* fuchsii in tissue culture. Acta Universitatis Latviensis, Biology 745: 17-23. http://eeb.lu.lv/EEB/2008/Jakobsone_1.pdf

Jakobsone G, Belogrudova I, Megre D. 2010. *Dactylorhiza* fuchsii (Druce) Soó As A Model Object In In Vitro Culture Study For Development Of Terrestrial Orchids. Acta Biol Univ Daugavp, Suppl. 2: 41 - 48

Janečková P, Wotavová K, Schödelbauerová I, Jersáková J, Kindlmann P. 2006. Relative effects of management and environmental conditions on performance and survival of populations of a terrestrial orchid, *Dactylorhiza* majalis. Biol Conserv 129 (1): 40-49. DOI: 10.1016/j.biocon.2005.09.045

Kirillova IA, Kirillov DV. 2013. Features of biology, reproduction and structure of cenopopulations of *Dactylorhiza* fuchsii sl (Orchidaceae) at the northern limit of distribution. Botanicheskij zhurnal 98 (2): 75-90.

Kosolapova NV, Gudovskikh YV, Egoshina TL, Kislitsyna AV, Luginina EA. 2021. To the characteristic of cenopopulations *Dactylorhiza Dactylorhiza* Fuchsii (Druce) Soo of the Middle and Southern Taiga. IOP Conf Ser: Earth Environ. Sci. 901: 012025

Kotukhov YA, Danilova AN, Anufriyeva OA, Suleimenov AN, Sumbembayev AA, Kubentaev SA. 2018. Ecological and biological features of *Cypripedium* at Katon-Karagay State National Natural Park. Plant Arch 18(2): 1499-1502.

Kupriyanov OA, Kupriyanov AN, Abduova AA, Yessengeldi A, Sataev MI, Moshkalov BM, Tolegen M. 2019. Coenoflora and Spiraeanthus schrenkianus Maxim population structure in the mountains of Boraldaytau. EurAsian J BioSci 13 (2): 1205-1213.

Landolt E. 1977. Okologische Zeigerwerte zur Schweizer Flora. Veroff. Geobot. Inst. Rubel. H.64. Zurich: Stiftung Riibel.

Naczk AM, Kowalkowska AK, Wiśniewska N, Haliński ŁP, Kapusta M, Czerwicka M. 2018. Floral anatomy, ultrastructure and chemical analysis in *Dactylorhiza incarnata/maculata* complex (Orchidaceae). Bot J Linn Soc 187 (3): 512-536. DOI: 10.1093/botlinnean/boy027

Peakall R, Smouse PE. 2012. GenAlEx tutorials-part 2: genetic distance and analysis of molecular variance (AMOVA). Bioinformatics 28: 2537-2539.

Peet RK, Wentworth TR, White PS. 1998. A flexible, multipurpose method for recording vegetation composition and structure. Castanea 63 (3): 262-274.

Ponomarev EI, Kharuk VI. 2016. Wildfire occurrence in forests of the Altai-Sayan region under current climate changes. Contemp Probl Ecol 9 (1): 29-36. DOI: 10.1134/S199542551601011X

POWO. 2022. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet; http://www.plantsoftheworldonline.org/Retrieved 15 January 2022.

Red Book of Kazakhstan. 2014. Ed. 2nd, revised and enlarged. Volume 2: Plants (team of authors). Astana: LLP "ArtPrint.

Sultangazina GZh, Hrustaleva IA, Kuprijanov AN. 2013. Redkie rastenija nacional'nogo prirodnogo parka «Burabaj» Vestnik KazNU. [Rare plants of the National Natural Park "Burabay"] Vestnik KazNU ser. Jekol. - KazNU Bulletin. ser. Ekol.3 (39): 264-270. [Russian]

Sumbembayev A, Abugalieva S, Danilova A, Matveyeva E, Szlachetko D. 2021. Flower morphometry of members of the genus *Dactylorhiza* Necker ex Nevski (Orchidaceae) from the Altai Mountains of Kazakhstan. Biodiversitas 22 (8): 3545-3555. DOI: 10.13057/biodiv/d220855

Takhtajan AL. 2009. Flowering Plants. Springer, The Nederlands.

Taraška V, Batoušek P, Duchoslav M, Temsch EM, Weiss-Schneeweiss H, Trávníček B. 2021. Morphological variability, cytotype diversity, and cytogeography of populations traditionally called *Dactylorhiza fuchsii* in Central Europe. Plant Syst Evol 307 (4): 1-21. DOI: 10.1007/s00606-021-01770-3

Tyteca, Gathoye JL. 1999. Morphometric analysis of *Dactylorhiza occitanica* and related populations from eastern France (Orchidaceae). Belgian J Bot 132 (2): 158-174.

Vakhrameeva MG. 2006. Ontogeny and population dynamics of *Dactylorhiza* fuchsii (Orchidaceae). Botanicheskij zhurnal 91 (11): 1683-1695.

Wróblewska A, Szczepaniak L, Bajguz A, Jędrzejczyk I, Tałałaj I, Ostrowiecka B, Mirski, P. 2019. Deceptive strategy in *Dactylorhiza* orchids: multidirectional evolution of floral chemistry. Annals of botany 123 (6): 1005-1016. DOI: 10.1093/aob/mcz003

Zlobin Yu.A. 1989 Principles and methods of coenotic plant populations. Kazan University, Kazan.

Table S1. Species and genera in families found in Sayan-Altai Mountains, Kazakhstan

Species	**Abundance***				**Occurrence of species, %**
	Pop. 1	**Pop. 2**	**Pop. 3**	**Pop. 4**	
Equisetaceae Michx. ex DC					
Equisetum arvense L.	3-4		2-5	2	40
Equisetum fluviatile L.				2	10
Equisetum palustre L.	2				10
Equisetum pratense Ehrh.	2		2	2	25
Equisetum ramosissimum Desf.	2				10
Equisetum sylvaticum L	3	3-4		4	25
Pinaceae Lindl.					
Abies sibirica Ledeb.			2-4		35
Picea obovata Ledeb.	4		2-3		25
Pinus sibirica Du Tour	2		2		25
Ranunculaceae Juss.					
Aconitum septentrionale Koelle			2		10
Aconitum volubile Pall. ex Koelle	1	1			10
Aconitum anthora L.			1		10
Clematis alpina (L.) Mill.	2				10
Caltha palustris L.			1		10
Clematis integrifolia L.				1	10
Ranunculus acris L.			1	2-3	25
Ranunculus grandifolius C.A. Mey			1	1	10
Ranunculus krylovii Ovcz.	1			1	10
Ranunculus monophyllus Ovez.	1				10
Ranunculus repens L.				2	10
Thalictrum flavum L.		2	2		15
Thalictrum foetidum L.	1		2		15
Thalictrum isopyroides C.A. Mey.			2		10
Thalictrum minus L.	2			2	10
Thalictrum simplex L	3	2	2	2	40
Trollius altaicus C.A. Mey			2-3		25
Trollius asiaticus L.				2	10
Paeoniaceae Rudolphi					
Paeonia anomala L.	2				10
Papaveraceae Juss.					
Chelidonium majus L.	1	1			15
Caryophyllaceae Juss.					
Cerastium arvense L.			2		10
Cerastium pauciflorum Stev. ex Ser.	1				10
Dichodon cerastoides (L.) Reichenb.	1			2	15
Gypsophila paniculata L.	1		1		15
Silene chalcedonica (L.) E.H.L. Krause	1			1	15
Silene latifolia Poir.	1-2			2	35
Stellaria bungeana Fenzl	1-2		1	1	35
Stellaria graminea L.				1-2	15
Polygonaceae Juss.					
Persicaria bistorta (L.) Samp.	2			2	15
Persicaria vivipara (L.) Ronse Decr.	3	2			15
Rumex acetosa L.			1	2	15
Rumex acetosella L.				2	10
Rumex aquaticus L.	2	2	1		25
Rumex crispus L.			1		10
Rumex confertus Willd.				1	10
Betulaceae Gray					
Betula pendula Roth	3		2-3		25
Betula verrucosa Ehrh.	3	3	3-4	3	75
Betula microphylla Bunge			3		10
Hypericaceae Juss.					
Hypericum perforatum L.	2	2-3			15
Hypericum hirsutum L.			1		10
Ericaceae Juss.					
Empetrum nigrum L.	4				10
Vaccinium microcarpum (Turcz. ex Rupr.) Schmalh.	2				10
Vaccinium vitis-idaea L.	4				10
Pyrola rotundifolia L.	2				10
Primulaceae Vent.					
Primula veris subsp. *macrocalyx* (Bunge) Lüdi			2		10
Androsace filiformis Retz.			2		10
Violaceae Batsch					
Viola altaica Ker Gawl.			1		10
Salicaceae Mirb.					
Populus tremula L.			2-3		15
Salix bebbiana Sarg.	2				10
Salix caprea L.	1		2	2	40
Salix cinerea L.			2		10
Salix pyrolifolia Ledeb.	2				15
Salix viminalis L.	2-3		2-3	2	40
Brassicaceae Burnett					
Draba sibirica (Pall.) Thell.	1	2			10
Hesperis matronalis L.				1	10
Thlaspi arvense L.				1	10
Urticaceae Martinov					
Urtica dioica L.				2	10
Euphorbiaceae Juss.					
Euphorbia mellifera Aiton			2		10
Glossulariaceae DC.					
Ribes nigrum L.		2			10
Ribes rubrum L.			2		15
Droseraceae Salisb.					
Drosera rotundifolia L.	1				10
Rosaceae Juss.					
Agrimonia eupatoria subsp. *asiatica* (Juz.) Skalický				1	10
Agrimonia pilosa Ledeb.	2	2		1	25
Alchemilla altaica Juz.			1		15
Alchemilla bungei Juz.			1		10
Alchemilla sibirica Zämelis		2		1-2	25
Alchemilla xanthochlora Rothm.		2	2	2	35
Cotoneaster melanocarpus Fisch. Ex Blytt		3			10
Crataegus chlorocarpa Lenne & C. Koch	2	3			15
Crataegus sanguinea Pall	2				10
Filipendula ulmaria (L.) Maxim.	2-4	2	2	2	50
Fragaria vesca L.		2			10
Fragaria viridis (Duch.) Weston		2			10
Geum rivale L.		2	1	2	35
Malus baccata (L.) Borkh	1-2				15
Prunus padus L.	1-2	1			25
Dasiphora fruticosa (L.) Rydb.	2		2		15
Potentilla anserine (L.) Rydb.				1	10
Potentilla chrysantha Trevir.			2	1	15
Potentilla erecta (L.) Raeusch.			1		10
Rosa acicularis Lindl.	2-3	3			25
Rubus saxatilis L.	5	2-3			15
Sanguisorba alpina Bunge			1-2		15
Sanguisorba officinalis L.	1	2	2	2	40
Sorbus aucuparia subsp. *sibirica* (Hedl.) Krylov			2-3		25
Spiraea media Schmidt	2		2-3		40

Onagraceae Juss.					
Epilobium angustifolium L.			1-3		25
Epilobium palustre L.			1		10
Fabaceae Lindl.					
Trifolium hybridum L.		2			10
Trifolium repens L.		2	2		35
Caragana arborescens Lam.			2		10
Lathyrus gmelinii Fritsch	1-2	1			25
Lathyrus emodi (Fritsch) Ali			1-3		25
Lathyrus pratensis L.	2				15
Melilotus officinalis (L.) Pall.			1		10
Lathyrus pannonicus subsp. *collinus* (J. Ortmann) Soo			1		10
Trifolium pratense L.			2	3	35
Vicia sepium L.	3	2	2		25
Oxalidaceae R. Br.					
Oxalis acetosella L.			1		10
Geraniaceae Juss.					
Geranium albiflorum Ledeb.			2		15
Geranium collinum Stephan ex Willd			2		15
Geranium pratense L.			2		15
Geranium pseudosibiricum J. Mayer	1	3			15
Balsaminaceae A. Rich.					
Impatiens noli-tangere L.			1-2		15
Polygolaceae R. Br.					
Polygala comosa Schkuhr		1			10
Celastraceae R.Br.					
Parnassia palustris L.			2		15
Apiaceae Lindl.					
Aegopodium alpestre Ledeb.			1		10
Angelica archangelica subsp. *decurrens* (Ledeb.) Kuvaev	2		1		15
Angelica sylvestris L.	2	2	2		25
Anthriscus sylvestris (L.) Hoffm.			1		10
Bupleurum longifolium L. subsp. *aureum* (Fisch. ex Hoffm.) Soo			1-2		15
Carum carvi L.		1	1	1	25
Heracleum sphondylium subsp. *montanum* (Schleich. ex Gaudin) Briq			2		10
Heracleum sphondylium subsp. *sibiricum* (L.) Simonk.			2		10
Schulzia crinita (Pall.) Spreng.			1		10
Sium sisarum L.			1		10
Caprifoliaceae Juss.					
Linnaea borealis L.		2	1		15
Lonicera caerulea subsp. *altaica* (Pall.) Gladkova			2		10
Lonicera tatarica L.	2	1			25
Adoxaceae E. Mey.					
Viburnum opulus L.		2			10
Rubiaceae Juss.					
Galium boreale L.			1		15
Galium verum L.	2			1	15
Gentinaceae Juss.					
Swertia perennis L.			1-2		15
Polemoniaceae Juss.					
Polemonium caeruleum L.			1		10
Boraginaceae Juss.					
Cynoglossum officinale L.			2	1	35
Lappula microcarpa (Ledeb.) Guerke			2		10
Lappula squarrosa (Retz.) Dumort.			1		10
Myosotis laxa subsp. *caespitosa* (Schultz) Hyl. ex Nordh.			2		10
Myosotis krylovii Serg.			2	2	15
Myosotis scorpioides L.			1-2	2	25
Pulmonaria mollis Wulf. ex Hornem		2	1		25

Scrophulariaceae Juss.					
Scrophularia altaica Murr.			2		10
Orobanchaceae Vent.					
Pedicularis altaica Steph. ex Stev.			2		25
Pedicularis resupinata L.				2	10
Pedicularis proboscidea Stev.	2		1		15
Rhinanthus serotinus subsp. *aestivalis* (N.W. Zinger) Dostál			2		15
Rhinanthus borbasii subsp. *songaricus* Soó	1		2		10
Odontites vulgaris Moench			1		15
Plantaginaceae Juss.					
Linaria vulgaris Mill.	1			1	10
Plantago media L.			2		10
Veronica anagallis-aquatica L.			2		10
Lamiaceae Martinov					
Lamium album L.			1		15
Mentha longifolia var. *asiatica* (Boriss.) Rech.f.	2				10
Mentha arvensis L.			2		10
Mentha longifolia (L.) L.			1		10
Nepeta nuda L.				1	10
Origanum vulgare L.			1		10
Phlomoides tuberosa (L.) Moench			2		10
Phlomoides alpina (Pall.) Adyl., R. Kam. & Machmedov			1		10
Prunella vulgaris L.		3	1	1-3	35
Stachys palustris L.			1		10
Campanulaceae Juss.					
Campanula stevenii subsp. *altaica* (Ledeb.) Fed.			2		10
Asteraceae Bercht. & J. Presl					
Achillea millefolium L.	1		2		10
Artemisia vulgaris L.			1		10
Bidens tripartita L.			1		10
Parasenecio hastatus (L.) H.Koyama			1-2		25
Cirsium helenioides (L.) Hill			2-3		35
Cirsium arvense (L.) Scop.			2		10
Crepis sibirica L.	1	1	1		15
Hieracium dublizkii B. Fedtsch. & Nevski			1		15
Inula britannica L.	2		1-2		25
Ligularia altaica DC.			1-2		15
Ligularia robusta (Ledeb.) DC.	2				10
Gnaphalium sylvaticum L.			2		10
Saussurea parviflora (Poir.) DC.	2				10
Saussurea frolowii Ledeb.			2		10
Sonchus arvensis L.	3		1-2		40
Rhaponticum carthamoides (Willd.) Iljin			2		10
Tanacetum tanacetoides (DC.) Tzvel			1		10
Taraxacum campylodes G.E. Haglund				2	10
Tussilago farfara L.	2-3	4	1-3		35
Juncaginaceae Rich.					
Triglochin palustris L.	2				10
Melanthiaceae Batch ex Borkh.					
Veratrum lobelianum Bernh.	2		1-2		35
Paris quadrifolia L.	1				10
Amaryllidaceae J.St.-Hil. nom. cons. (Alliaceae Borkh.)					
Allium microdictyon Prokh.			2-4		25
Allium ledebourianum Schults. & Schult. fil.			3		10
Orchidaceae Juss.					
Cypripedium macranthos Sw.	1-3				15
Dactylorhiza fuchsii (Druce) Soo	2-3	2-3	2-3	2-3	100
Dactylorhiza salina (Turcz. ex Lindl.) Soo				3	10

Dactylorhiza incarnata (L.) Soo			2		15
Epipactis palustris (L.) Crantz	2				10
Gymnadenia conopsea (L.) R. Br.	1				10
Herminium monorchis (L.) R. Br.	1				10
Neottia ovata (L.) Bluff & Fingerh	1	2			15
Orchis militaris L.	1				15
Juncaceae Juss.					
Juncus compressus Jacq.	2	2	3-4	2	50
Juncus filiformis L.		2			10
Juncus gerardii Loisel.		1		1-2	25
Luzula campestris (L.) DC.				2	10
Cyperaceae Juss.					
Blysmus rufus (Huds.) Link		2		1	15
Carex acuta L.				1	10
Carex alba Scop.	2				10
Carex pamirensis subsp. *dichroa* Malyschev	2				10
Carex disticha Huds.		2		2-4	25
Carex elongata L.			3-4		25
Carex nigra subsp. *juncea* (Fr.) Soó		3		5	15
Carex pediformis var. *macroura* (Meinsh.) Kük.	2	2		2	25
Carex atherodes Spreng			2		10
Carex cespitosa L.			1		10
Carex canescens L.				2	10
Carex pauciflora Lightf.			1		10
Carex nigra (L.) Reichard.		1			10
Carex vulpine L.				2	10
Eleocharis palustris (L.) Roem. & Schult.	1		1	2	15
Poaceae Barnhart					
Agrostis stolonifera L.			1		10
Agrostis gigantea Roth			2-3		25
Agrostis clavata Trin.			1		10

Alopecurus aequalis Sobol.	1	1	1		25
Alopecurus arundinaceus Poir.		1			10
Beckmannia eruciformis (L.) Host		1		2	15
Calamagrostis epigejos (L.) Roth	5			4	15
Calamagrostis purpurea (Trin.) Trin.		2			10
Calamagrostis stricta (Timm) Koeler	2		2		15
Calamagrostis obtusata Trin.		1		1	15
Catabrosa aquatica (L.) Beauv.				1	10
Dactylis glomerata L.	2	2	2		40
Deschampsia cespitosa (L.) Beauv	2		2	2-3	35
Elymus caninus (L.) L.	2				10
Elymus mutabilis (Drob.) Tzvel.	2		2		15
Elymus repens (L.) Gould	1		2	2	35
Festuca altissima All.	1		2-3	1	35
Festuca pratensis (De Not.) Hegi.	2	3			15
Hierochloe odorata (L.) P.Beauv.	2				10
Hordeum brevisubulatum (Trin.) Link	2				10
Melica altissima L.	2				15
Melica nutans L.	2	1		2	25
Milium effusum L.	2			2	15
Phalaris arundinacea L.				1	10
Phleum alpinum L.			1-2		10
Phleum phleoides (L.) Karst.	2		2-3		33
Phragmites australis (Cav.) Trin. Ex Steud.	2		3		25
Poa angustifolia L.	1			2	25
Poa nemoralis L.		3			10
Poa palustris L.	2	1	1	2-3	35
Poa pratensis L.	2	1	2	2	35
Poa remota Forsell.	1		1		15

Note: * Abundance on the Broun-Blanquet Scale (1964): 1: extremely rare (5%), 2: rare (5-20%), 3: diffusely (20-40%), 4: frequently (40-60%), 5: abundantly (60-100%).