The structure of variability of traits of seed productivity of *Allium charadzeae* Tschlok in the mountainous conditions of Dagestan

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Abstract. As a result of the experimental studies, results were obtained on the variability of the traits of seed productivity of the narrow-local endemic of Dagestan – *Allium charadzeae* under various conditions along the altitude gradient. Analysis of the data obtained revealed significant differences in the indicators of seed productivity of individuals. The actual seed productivity is significantly inferior to the potential, which indicates a low degree of realization of the potential for seed formation in mountainous conditions. With an increase in the height above sea level of the experimental plots, the absolute indicators of traits of seed productivity decrease (the number of fruits in the umbrella from 14.9 to 8.5, the number of flowers in the inflorescence from 24.7 to 12.1, the number of seeds in the umbrella from 26.6 up to 19). At the same time, the relative indicators, the percentage of fruit blossoming from 60.5 to 71.2 and the coefficient of seed production from 0.17 to 0.27 increases. As a result of the analysis of variance, a significant influence of the conditions of the year and altitude above sea level on the studied characteristics was revealed.

1 Introduction

The study and conservation of biological diversity, the identification of species adaptations in the process of evolution, as well as adaptive traits and reactions, methods of survival are among the most important scientific tasks in modern biology. Various natural and climatic conditions of Dagestan, in particular the strong dissection of the relief and the presence of geographical barriers, are the reasons for the great floristic diversity and endemism, which are most characteristic of the communities of upland xerophytes. In this regard, the question of studying endemic, rare and endangered plant species becomes relevant, since only a comprehensive study of the biology of species, intra- and inter-population variability, tactics and strategies of survival can provide an objective assessment of the state of cenopopulations of endemic, rare species and organize their effective protection. Some endemic species with reduced adaptive capabilities disappear, being unable to adapt to changing environmental conditions, unable to withstand competition from other species. Due to their extreme ecological specialization, they are easily vulnerable and therefore

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require special attention [1].

The subgenus *Rhizirideum* of the genus *Allium* in Dagestan is represented by two widespread species (*Allium saxatile* M. Bieb. and *Allium globosum* M. Bieb. ex Redoute) and a group of local endemics [2], the taxonomic status of which is still controversial (*Allium daghestanicum* Grossh., *Allium samurense* Tscholok., *Allium gunibicum* Miscz. ex Grossh., *Allium mirzojevii* Tscholok., and *Allium charadzeae* Tscholok.).

In the study of the taxonomy of this genus, the method of molecular genetic analyzes has been widely used in recent years, including the use of some local endemics of the Caucasian flora for this purpose [3–6].

Particular attention should be paid to the study of seeds and seed productivity as the basis for the reproduction and introduction of endemic species. The seeds of blossoming plants are the main elements of a system of adaptive or reproductive strategies. Among the characteristics of seeds closely related to the reproductive strategy, their size and weight are important. The quantitative characteristics of seeds are also of interest in the development of seed science of introduced species. Qualitative characteristics of seeds (shape, surface traits) are also used in the taxonomy of the genus *Allium* [7].

Seed productivity is one of the most important indicators of the adaptation of a species to specific habitat conditions. Determination of the potential seed productivity and the degree of its realization makes it possible to characterize the reproductive capabilities of the species, its ability to reproduce itself in cenopopulations. The ratio between the indicators of seed productivity, or the coefficient of seed production, is considered a reliable indicator of the adaptation of a species to certain environmental conditions and a criterion for successful seed reproduction and the well-being of the population [8–10]. Experimental studies allow a deeper study of the features of the formation of the population structure of species, to reveal the patterns of micro-evolutionary processes in a changing environment along the altitude gradient, depending on the combination of environmental factors (abiotic and biotic).

This paper presents an analysis of the variability of the traits of seed productivity of the narrow-local Dagestan endemic *Allium charadzeae*, collected from different heights above sea level and grown under experimental conditions on two bases.

2 Methods

The material for the research was *A. charadzeae* plants obtained by sowing seeds collected at different altitudes (1000, 1240 and 1450 meters above sea level) in the vicinity of the village of Arkas, Buinaksky district of the Republic of Dagestan. *A. charadzeae* is a narrow-localized endemic to Dagestan, found in the middle mountain zone. It grows on rocky places on the southwestern slopes, within 1200–1500 m above sea level. Experimental studies were carried out for three years (2018–2020) at various altitudes at the Tsudahar (1100 m) and Gunib (1750 m) experimental bases of the Mountain Botanical Garden. Seed productivity was assessed according to generally accepted methods [9, 10].

The potential seed productivity was determined by the number of ovules formed on the plant, and the real one was determined by the number of ripened seeds. Percentage of fruit blossoming – the ratio of the number of fruit set to the number of flowers in the inflorescence, expressed as a percentage. The coefficient of semenification is the ratio of the indicators of the real seed productivity to the potential one. The reproductive effort efficiency is the ratio of the mass of seeds in the inflorescence to the mass of the inflorescence. To analyze the dimensional, numerical and weight characteristics, 10 umbrellas were collected in the phase of full seed ripening. In laboratory conditions, cameral processing (measurements and counting) of the collected material was carried out. The mass of the inflorescence, the mass of seeds in the inflorescence, and the mass of 100

seeds were determined by weighing on an electronic balance.

Phenological observations were carried out throughout the growing season according to the generally accepted method, which is based on the registration of successive phases of development and growth of plants, characterized by clearly expressed morphological changes during the year [11]. The beginning of the mass onset of the phase was considered the moment at which at least 50% of the composition of the sample of plants taken under observation entered.

Statistical processing of the obtained data was carried out using variance, correlation, discriminant analyzes [12], using the statistical software package Statistica v. 13.

3 Results

A. charadzeae – a narrow-local Dagestan endemic was described by N. B. Cholokashvili [13] based on the collection of herbarium material above the village of Arkas (Untsukulsky district) near a spring on the rocks, referring to the section Daghestanica (Tschlok.). However, later by G. A. Kudryashova [14], this species was reduced to the synonym *A. gunibicum*. The studies carried out – morphological and molecular genetic [15, 16] revealed that the description as a separate species was justified.

The degree of conformity of ecological conditions and the vital state of the population can be assessed on the basis of the potential and actual seed productivity. The results of studies of the variability of the traits of seed productivity of *A. charadzeae* at different altitude levels are shown in Table 1.

Table 1. Characteristics of traits of seed productivity of *Allium charadzeae* (population in the vicinity of the village of Arkas) when introduced at different altitude levels.

Traits	Tsudahar (1100 m)		Gunib (1750 m)	
	X±Sx	CV	X±Sx	CV
Mass of inflorescence (mg)	93.0±2.78	9.5	46.5±1,72	11.7
Number of fruits (pcs.)	14.9±0.98	20.8	8.5±0,43	15.9
Number of flowers (pcs.)	24.7±1.62	20.7	12.1±0,66	17.2
Number of seeds on inflorescence (pcs.)	26.6±1.90	22.6	19,0±1,50	24.9
Mass of seeds on inflorescence (mg)	32.0±2.91	28.8	21.2±1,55	23.1
Mass of 100 seeds (mg)	121.2±8.24	21.5	114.4±7,97	22.0
Percentage of fruit blossoming (%)	60.5±1.70	8.9	71.2±3,56	15.8
Coefficient of semenification (%)	0.19±0.025	41.4	0.27±0,029	34.3
Reproductive effort efficiency (%)	0.34±0.031	28.7	0.45±0,023	16.3
Number of seeds per one fruit (pcs.)	1.9±0.26	42.6	2.3±0,21	29.0

Note: X – mean, ± Sx – standard error, CV – coefficient of variation in % (the same note in Tables 3, 6, 9).

Studies have shown that with an increase in the height above sea level of the experimental patch, the average values of the weight and numerical traits of seed productivity of *A. charadzeae* decrease (Table 1). Mass of inflorescence from 93 mg to 46.5 mg; the number of fruits from 14.9 to 8.5 pieces; the number of flowers from 24.7 to 12.1; the number of seeds in the umbrella from 26.6 to 19.0; seed mass per inflorescence from 32.0 mg to 21.2 mg; the mass of 100 seeds decreases slightly from 121.2 mg to 114.4 mg. At the same time, the relative indicators, the percentage of fruit blossoming from 60.5 to 71.2, the coefficient of semenification from 0.17 to 0.27, and the reproductive effort effeciency of from 0.34 to 0.45 increases. The most variable traits are: the mass of seeds in the inflorescence, the coefficient of seed production, the number of seeds per one fruit (CV = 23.1–42.6%), and the most stable traits are the percentage of fruit blossoming and the mass of the inflorescence (CV = 8.9–15.8%).

To clarify the effect of the conditions of the test sites at different altitude levels, an analysis of variance was carried out. The results of the analysis showed that the factor "height of the experimental patch" significantly and highly reliably affects the characteristics of the inflorescence mass, the number of fruits, the number of flowers, the number of seeds in the inflorescence, the mass of seeds in the inflorescence, the percentage of fruit blossoming, the reproductive effort efficiency. The share of the influence of this factor is from 29.1 to 91.8%. No reliable influence of the factor on the traits was found for the mass of 100 seeds and the number of seeds per one fruit.

Table 2. Results of univariate analysis of variance for traits of seed productivity of *Allium charadzea*e (Arkas population) when introduced under the conditions of experimental bases.

Traits	The source of variability is the "height of the experimental patch"			
	SS	MS	F–criterion	h^2
Mass of inflorescence (mg)	10811.25	10811.25	201.8***	91.8
Number of fruits (pcs.)	204.80	204.80	35.7***	66.5
Number of flowers (pcs.)	793.80	793.80	51.9***	74.3
Number of seeds on inflorescence (pcs.)	288.80	288.80	9.8**	35.3
Mass of seeds on inflorescence (mg)	583.20	583.20	10.7**	37.3
Mass of 100 seeds (mg)	230.25	230.25	0.4	–
Percentage of fruit blossoming (%)	573.52	573.52	7.4*	29.1
Coefficient of semenification (%)	0.03	0.03	4.0	–
Reproductive effort efficiency (%)	0.06	0.06	7.7*	30.0
Number of seeds per one fruit (pcs.)	0.61	0.61	1.1	–

Note: SS – sum of squares of deviations, MS – middle square, h^2 – factor influence (the same note in Tables 4, 7).

At different altitude levels, the ecological factors of the habitats of plant species vary greatly in different years within the same time periods. Among the multitude of abiotic factors, the main and significant role in the variability is played by the terrain, the exposure of the slope, the steepness of the slope, including the height difference. And as a result of fluctuations in different-year environmental conditions in a particular cenopopulation of plants, variability of the characteristics of individuals of this species arises. How the temperature changed over the time of observations in 2017–2019 at the Tsudahar experimental base is shown in Figure 1.

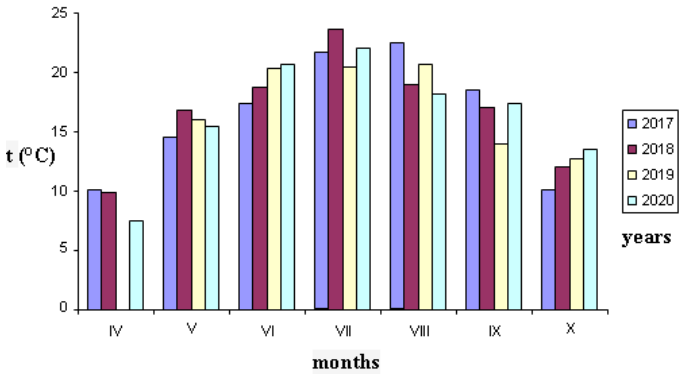

Fig. 1. Average temperatures in (° C) by months from April to October at the Tsudahar experimental base for 2017–2020.

Characteristics of the traits of seed productivity of *A. charadzeae* in different years are presented in Table 3. Indicators of seed productivity are different from year to year. The maximum values were obtained in 2018, and by 2020 they are decreasing.

Table 3. Characteristics of traits of seed productivity of *Allium charadzeae* (Arkas population) in different years.

Traits	2018		2019		2020	
	X±Sx	CV	X±Sx	CV	X±Sx	CV
Mass of inflorescence (mg)	109.4±11.92	34.5	93.0±2.78	9.5	59.6±5.19	27.5
Number of fruits (pcs.)	16.9±1.66	31.0	14.9±0.98	20.8	9.0±0.71	25.1
Number of flowers (pcs.)	25.4±2.13	26.5	24.7±1.62	20.7	11.0±0.87	25.0
Number of seeds on inflorescence (pcs.)	41.7±6.46	49.0	26.6±1.90	22.6	25.0±3.07	38.9
Mass of seeds on inflorescence (mg)	43.2±7.49	54.8	32.0±2.91	28.8	32.1±3.67	36.2
Mass of 100 seeds (mg)	102.2±6.45	19.9	121.2±8.24	21.5	130.5±4.98	12.1
Percentage of fruit blossoming (%)	66.0±2.03	9.8	60.5±1.70	8.9	82.3±2.84	10.9
Coefficient of semenification (%)	0.27±0.032	37.9	0.19±0.025	41.4	0.38±0.031	26.0
Reproductive effort efficiency (%)	0.37±0.035	29.3	0.34±0.031	28.7	0.54±0.033	19.6
Number of seeds per one fruit (pcs.)	2.4±0.25	32.8	1.9±0.26	42.6	2.8±0.20	23.3

The decrease in the number of fruits of set seeds can be caused by several probable reasons, including unfavorable environmental conditions during the period of laying of reproductive organs and fruit formation and an insufficient number of pollinators in 2020. At the same time, the mass of 100 seeds, the percentage of fruit blossoming, the coefficient of semenification, the reproductive effort efficiency of increase.

As a result of the analysis of variance, it turned out that different-year conditions significantly and highly reliably affect the traits of inflorescence: mass of inflorescence, number of fruits, number of flowers, number of seeds in an inflorescence, mass of seeds in an inflorescence, and per mass of 100 seeds (Table 4).

Table 4. Results of univariate analysis of variance for traits of seed productivity of *Allium charadzeae*.

Traits	The source of variability is the “years”			
	SS	MS	F–criterion	h^2
Mass of inflorescence (mg)	9841.400	4920.700	7.60	39.8
Number of fruits (pcs.)	167.267	83.633	5.26	29.9
Number of flowers (pcs.)	467.267	233.633	8.08	41.5
Number of seeds on inflorescence (pcs.)	1520.067	760.033	4.15	24.0
Mass of seeds on inflorescence (mg)	1753.867	876.933	3.62	20.7
Mass of 100 seeds (mg)	3735.654	1867.827	4.12	23.8
Percentage of fruit blossoming (%)	274.254	137.127	1.99	–
Coefficient of semenification (%)	0.038	0.019	2.24	–
Reproductive effort efficiency (%)	0.007	0.003	0.40	–
Number of seeds per one fruit (pcs.)	1.525	0.763	1.16	–

The contribution of the relative component of the variance to the total is 20.7–41.5%. No reliable influence of the factor “years” on the traits of the percentage of fruit

blossoming, the coefficient of seed production, the reproductive effort efficiency of and the number of seeds per one fruit was found. To determine the relationships between the studied traits of seed productivity at different test sites in *A. charadze* individuals, the correlation coefficients were calculated (Table 4).

Correlation coefficients (r) between the traits of seed productivity of *A. charadzeae* tested in more severe conditions at an altitude of 1750 m above sea level (Gunib plateau), in most cases, increase (Table 5).

Table 5. Correlation coefficients between the traits of seed productivity of *A. charadzeae* in different test patches.

Traits	A	B	C	D	E	G	H
A							
B	0.74*** 0.67**						
C	0.81*** 0.72***	0.98*** 0.92***					
D	0.79*** 0.71***	0.56* 0.48*	0.43 0.44				
E	0.87*** 0.81***	0.46 0.26	0.31 0.26	0.87*** 0.77***			
F	0.68** 0.56*	0.12 -0.03	0.10 0.00	0.34 0.20	0.78*** 0.76***		
G	0.31 0.10	0.61** 0.47*	0.28 0.10	0.27 0.24	0.15 0.09		
H	0.36 0.23	-0.31 -0.15	-0.46 -0.24	0.61** 0.72***	0.54* 0.62**	0.36 0.21	
I	0.54* 0.31	-0.21 -0.20	-0.31 -0.25	0.63** 0.59**	0.83*** 0.78***	0.05 0.11	0.77*** 0.84***

Note: the upper numbers are the correlation coefficients at an altitude of 1750 m, the lower ones are the correlation coefficients at an altitude of 1100 m; traits: A – mass of inflorescence, B – number of fruits, C – number of flowers, D – number of seeds in an inflorescence, E – mass of seeds in an inflorescence, F – mass of 100 seeds, G – percentage of fruit blossoming, H – coefficient of semenification , I – reproductive effort efficiency; * – $P < 0.05$; ** – $P < 0.01$; *** – $P < 0.001$.

Between the signs of inflorescence (A – mass of inflorescence, B – number of fruits, C – number of flowers, D – number of seeds in an inflorescence, E – mass of seeds in an inflorescence), positive and reliable relationships were revealed in both test sites (1100 and 1750 m) – r = 0.67– 0.87. The traits behave relatively independently: the percentage of fruit blossoming, the mass of 100 seeds, and the coefficient of seed production from other studied traits. The mass of 100 seeds has positive reliable relationships with the traits of the mass of the inflorescence – r = 0.56–0.68, the mass of seeds in the inflorescence – r = 0.76–0.78 and the effectiveness of reproductive effort – r = 0.62–0.74. Reliable connections were found between the traits, the percentage of fruit flowering and the number of fruits – r = 0.47–0.61.

The degree to which the ecological conditions of modern habitats correspond to the biological requirements of the species and the vital state of the population can be assessed on the basis of the potential and actual seed productivity. Characteristics of the traits of seed productivity of three samples from different altitude levels of *A. charadzeae* are presented in Table 6.

Table 6. Characteristics of the traits of seed productivity of three samples of *A. charadze* during the introduction at the Tsudahar experimental base.

Traits	1000 m		1210 m		1480 m	
	X±Sx	CV	X±Sx	CV	X±Sx	CV
Mass of inflorescence (mg)	119.4±8.87	23.5	93.0±2.78	9.5	89.6±5.91	20.9
Number of fruits (pcs.)	20.0±1.28	20.3	14.9±0.98	20.8	14.6±1.15	24.8
Number of flowers (pcs.)	30.1±2.13	22.3	24.7±1.62	20.7	19.5±1.33	21.5
Number of seeds on inflorescence (pcs.)	37.5±3.43	28.9	26.6±1.90	22.6	29.5±2.46	26.4
Mass of seeds on inflorescence (mg)	44.6±6.11	43.3	32.0±2.91	28.8	44.1±3.55	25.5
Mass of 100 seeds (mg)	115.4±6.33	17.3	121.2±8.24	21.5	152.4±8.58	17.8
Percentage of fruit blossoming (%)	67.1±2.69	12.7	60.5±1.70	8.9	74.5±1.48	6.3
Coefficient of semenification (%)	0.22±0.024	35.1	0.19±0.025	41.4	0.25±0.018	22.6
Reproductive effort efficiency (%)	0.37±0.034	29.3	0.34±0.031	28.7	0.49±0.020	12.6
Number of seeds per one fruit (pcs.)	1.9±0.16	27.4	1.9±0.26	42.6	2.0±0.14	21.6

The analysis of the obtained data revealed significant differences in the parameters of seed productivity of *A. charadzea*e individuals (the number of semenification) both among themselves and the differences between the populations in terms of these indicators, depending on the height of the place of collection of the material. The factor "height of the material collection patch" is understood as the origin of samples collected along the vertical gradient, the aggregate of biotic and abiotic factors of the natural habitat, under the influence of which the formation of the genotype of the population took place. In a comparative analysis of the average values of some elements of seed productivity of samples of different heights, it was found that the traits of inflorescence (mass of inflorescence, number of fruits, number of flowers in an inflorescence, number of seeds in an inflorescence) decrease with an increase in the height of the collection patch. This significantly increases the mass of 100 seeds and the reproductive effort efficiency – the ratio of the mass of seeds to the mass of the inflorescence. The level of variability of the elements of seed productivity is different. The most variable are the traits: mass and number of seeds in the inflorescence, the coefficient of seed production. Less variable – the mass of 100 seeds, the percentage of fruit blossoming (Table 6).

As a result of the one-way analysis of variance for each of the studied characters, inter-population differentiation was revealed for a number of quantitative characters of *A. charadzeae* (Table 7).

Table 7. Results of univariate analysis of variance for traits of seed productivity of *Allium charadzeae* populations introduced at the Tsudahar experimental base.

Traits	The source of variability is the "height"			
	SS	MS	F–criterion	h^2
Mass of inflorescence (mg)	5321.867	2660.933	6.57**	32.7
Number of fruits (pcs.)	184.2	92.1	7.04**	34.3
Number of flowers (pcs.)	561.867	280.933	9.46***	41.2
Number of seeds on inflorescence (pcs.)	637.4	318.7	4.46*	24.8
Mass of seeds on inflorescence (mg)	1018.067	509.033	2.61	–
Mass of 100 seeds (mg)	7945.38	3972.69	6.56**	32.7

Percentage of fruit blossoming (%)	983.869	491.934	11.96***	47.0
Coefficient of semenification (%)	0.019	0.009	1.81	–
Reproductive effort efficiency (%)	0.123	0.061	7.27**	34.8
Number of seeds per one fruit (pcs.)	0.105	0.053	0.14	–

It turned out that the greatest contribution to inter-population differentiation during the introduction on the Tsudahar experimental base, taking into account the factor "height" (the place of collection of material), is made by the following characteristics: the number of flowers, the number of fruits, the percentage of fruit blossoming (Figure 2).

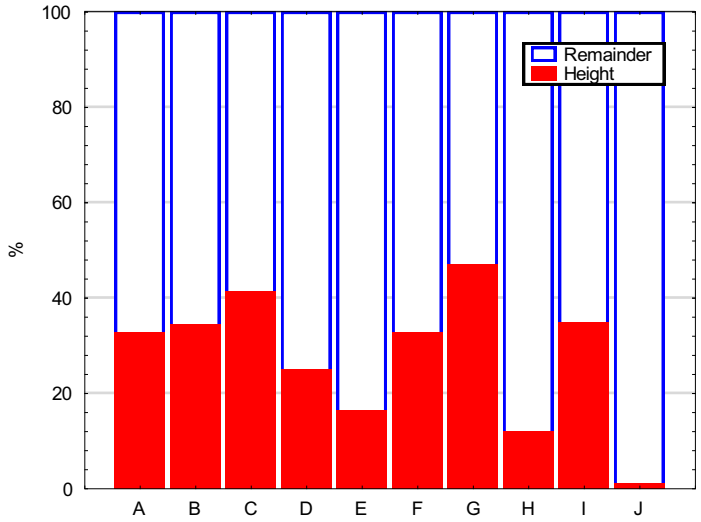

Fig. 2. Relative dispersion components (in %) based on the results of one-way analysis of variance based on traits of seed productivity of *Allium charadzeae*.

Note: A – mass of inflorescence, B – number of fruits, C – number of flowers, D – number of seeds in an inflorescence, E – mass of seeds in an inflorescence, F – mass of 100 seeds, G – percentage of fruit blossoming, H – coefficient of semenification , I – reproductive effort efficiency, J – number of seeds per one fruit.

Inter-population differences by traits: the mass of seeds in the inflorescence, the coefficient of semenification and the number of seeds per fruit are not reliable. Fruiting efficiency of *A. charadzeae* in the studied populations, the high is 60–75%.

Discriminant analysis showed that the greatest differentiation between populations is determined by the following features: mass of inflorescence, number of fruits. The rest of the traits turned out to be of little information (Table 8, Figure 3).

Table 8. Results of discriminant analysis with step-by-step elimination by the grouping variable – population.

Traits (n = 30)	**F**	**p**
In model		
Mass of inflorescence (mg)	64.79335	0,000000
Number of fruits (pcs.)	32,77203	0,000000
Not in model		
Coefficient of semenification (%)	1,758247	0,192996
Number of seeds on inflorescence (pcs.)	3,640754	0,040957
Percentage of fruit blossoming (%)	3,135225	0,060964
Reproductive effort efficiency (%)	0,853500	0,437962
Number of flowers (pcs.)	2,195704	0,132280

Mass of seeds on inflorescence (mg)	1,077549	0,355720
Mass of 100 seeds (mg)	5,048123	0,014404

Note: the number of variables is 9; grouping populations (3 gr.); in model F > 30,000, p <0.001.

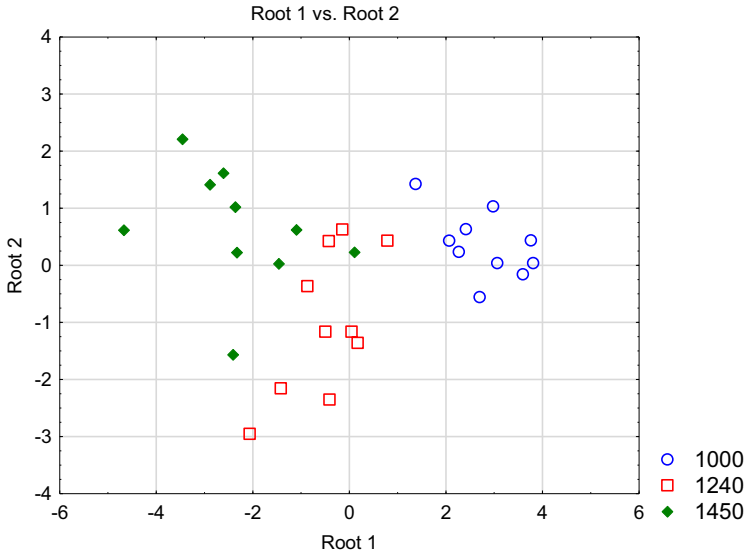

Fig. 3. Ordination of samples from different altitude levels of *Allium charadzeae* in the space of canonical roots based on the results of discriminant analysis.

Thus, the following diagnostic features have been determined: mass of inflorescence, number of fruits, which are the most delimiting populations of *A. charadzeae*.

4 Discussion

In our previous works, we carried out studies concerning the seed productivity of *A. gunibicum* [17]. A comparison of the seed productivity of two closely related species grown under the same culture conditions showed that the mass of inflorescence, the number of seeds per inflorescence, and the mass of seeds per inflorescence in *A. gunibicum* are significantly higher than in *A. charadzeae*. For the rest of the characteristics of seed productivity, these species do not differ significantly.

It is also interesting that high rates of fruit setting were also established for other species of the genus *Allium*. Thus, for *A. grande*, these indicators are 60–65% [18], for *A. gunibicu*m – 70–80% [17].

As a result of a comparative analysis of the variability of the traits of seed productivity of the narrow-local endemic of Dagestan, *A. charadzeae*, significant differences were revealed in the indicators of seed productivity of individuals (the number of fruits, ovules, seeds, the percentage of fruit blossoming, the coefficient of semenification) both among themselves within one year of research and over the years. As a result of the one-way analysis of variance, a significant influence of the conditions of the year, altitude, on the studied characteristics was revealed.

The system of correlations between morphological characters in plants changes under the influence of ecological conditions and genotypic rearrangements. Deterioration of environmental conditions and a decrease in adaptability in most cases causes a general increase in the strength of connections [19].

Correlation coefficients between the characteristics of *A. charadzeae* tested in more severe conditions at an altitude of 1750 m above sea level in the Gunib plateau, in most cases, increase. The mobilization of the system and tight connections between the elements ensure the preservation of the species in adverse conditions. The most efficiently separating populations were identified: the mass of the inflorescence and the number of fruits.

5 Conclusions

The study of the structure of variability of seed productivity is of great importance for understanding and evolution of the structure of populations in the process of speciation. It is known that high seed productivity is one of the conditions for maintaining the optimal number of individuals in populations. During the evolution of populations and the emergence of intra-specific differentiation, the very structure of seed productivity changes, i.e. the ratio between different components: between the number and weight of seeds, the number of fruits and seeds, and the number of generative shoots. The study of certain components of seed productivity makes it possible to judge the effectiveness of reproduction systems in specific environmental conditions.

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