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RESEARCH ARTICLE

The population structure of *Nepeta pamirensis* at different altitudes in the Pamirs (Tajikistan)

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Abstract

The structure of alpine plant populations is one of the main criteria for assessing the current state of alpine flora. Species of the genus *Nepeta*, most of which belong to alpine plants, can be universal objects for assessing changes in environmental conditions, including the impact of anthropogenic pressure. The article discusses the ontogenetic structure and population size in connection with the change in the life form of *Nepeta pamirensis* at different heights of the Pamirs (3060-4250 m a.s.l.). Our research showed that the ontogenetic spectra of different populations are different. These differences are linked to changes in the life form, the length of ontogenesis and how well seeds reproduce. Populations were studied using transects. The individual seed was taken as the counting unit. In total, 3 populations were studied and more than 750 individuals of different ontogenetic states were included in the analysis. The ontogenetic structure of populations was characterized using basic demographic indicators: the recovery index, ageing index, generative index and the ecological density index. Depending on the altitude gradient, the species was characterized by different efficiencies of seed reproduction, which determined the different densities of individuals in plant communities of distribution. In general, with an increase in the height of distribution of a species, the structure of the population became more stable.

Keywords

Populations; ontogenetic spectra; life forms; highlands; Pamirs; *Nepeta pamirensis*

Introduction

The flora and vegetation of the Pamirs have been studied for quite a long time as a biodiversity hotspot (1-9). Despite a wide range of studies, this mountainous region of Central Asia still remains poorly studied. Understanding the organization of species populations under the conditions of climate change and anthropogenic impact provides an opportunity to preserve the biodiversity of the Pamirs as a whole.

The study of altitude plants is impossible without considering their ecological features. In connection with this, population–ontogenetic methods are adequate and justified for determining the stability of the state of a population (10-14).

Among the altitude plants of the Pamirs, many are narrowly local; these species are confined to certain habitats and only some of them are more widely distributed. The phenomenon of such a wide amplitude adaptation in plants is poorly understood. *Nepeta pamirensis* Franch. at the Pamir-Alai, distributed at altitudes from 3400 m to 4900 m above sea level (a.s.l.), is part of various communities and can often be dominant (15, 16).

The biology and ecology of *N. pamirensis* have been rarely studied. It has only been established that in different regions and different altitudes of the Pamirs, the species has different life forms, while the duration of the ontogeny of the individuals also varies. At the lower boundary of its distribution, *N. pamirensis* has an herbaceous habit; above altitude h = 4000 m a.s.l., it is a dwarf semishrub; and at the limit of its distribution, *N. pamirensis* is a dwarf semishrub with a cushion-shaped growth form (17). Such features are considered mechanisms of the morphological adaptation of the species to the harsh conditions of the Pamirs.

The population organization of *N. pamirensis* at different altitudes in the Pamirs remains unclear. The study of the spatial and ontogenetic structure of *N. pamirensis* populations in the Pamirs has not been carried out before. The knowledge gained will expand the understanding of the diversity of *N. pamirensis* adaptation mechanisms and will become the basis for understanding the functioning of populations of other Pamirs alpine plants. The population-ontogenetic analysis (12, 13) used in the work can be used to characterize and assess the state of natural populations for similar species growing in other ecological and geographical conditions.

The aim of the study was to reveal the spatial and ontogenetic structure of *N. pamirensis* populations in the different conditions of the Pamirs. The objectives of the research included revealing the influence of the altitudinal gradient on the morphological parameters of *N. pamirensis* of different life forms, ontogenetic composition and population demography.

Materials and Methods

Studied species

N. pamirensis (family Lamiaceae) is distributed in the highlands of the Pamirs, the mountainous regions of the Hindu Kush, and the Himalayas framing it (15, 16). It grows on rubbly and coarse-stony slopes, screes, under rocks, in river valleys and sai and on mountain slopes, plateaus, and flat tops. The species is confined to the tragacanth, steppe, subalpine and alpine belts, often rising to the cryophyton zone.

Study area

According to the geomorphological and geological structure, the Pamirs are divided into 2 parts: the eastern and western. According to the totality of climatic conditions, the Eastern Pamirs belong to the cold deserts of the Central Asian type (7). This part of the Pamirs is characterized by large diurnal temperature fluctuations, very low relative humidity, and strong winds that dry out the surface layers of the soil and increase atmospheric drought. The Western Pamir is much warmer than the Eastern Pamir and has a West Asian climate (1, 7). We collected material from various habitats of the Pamirs

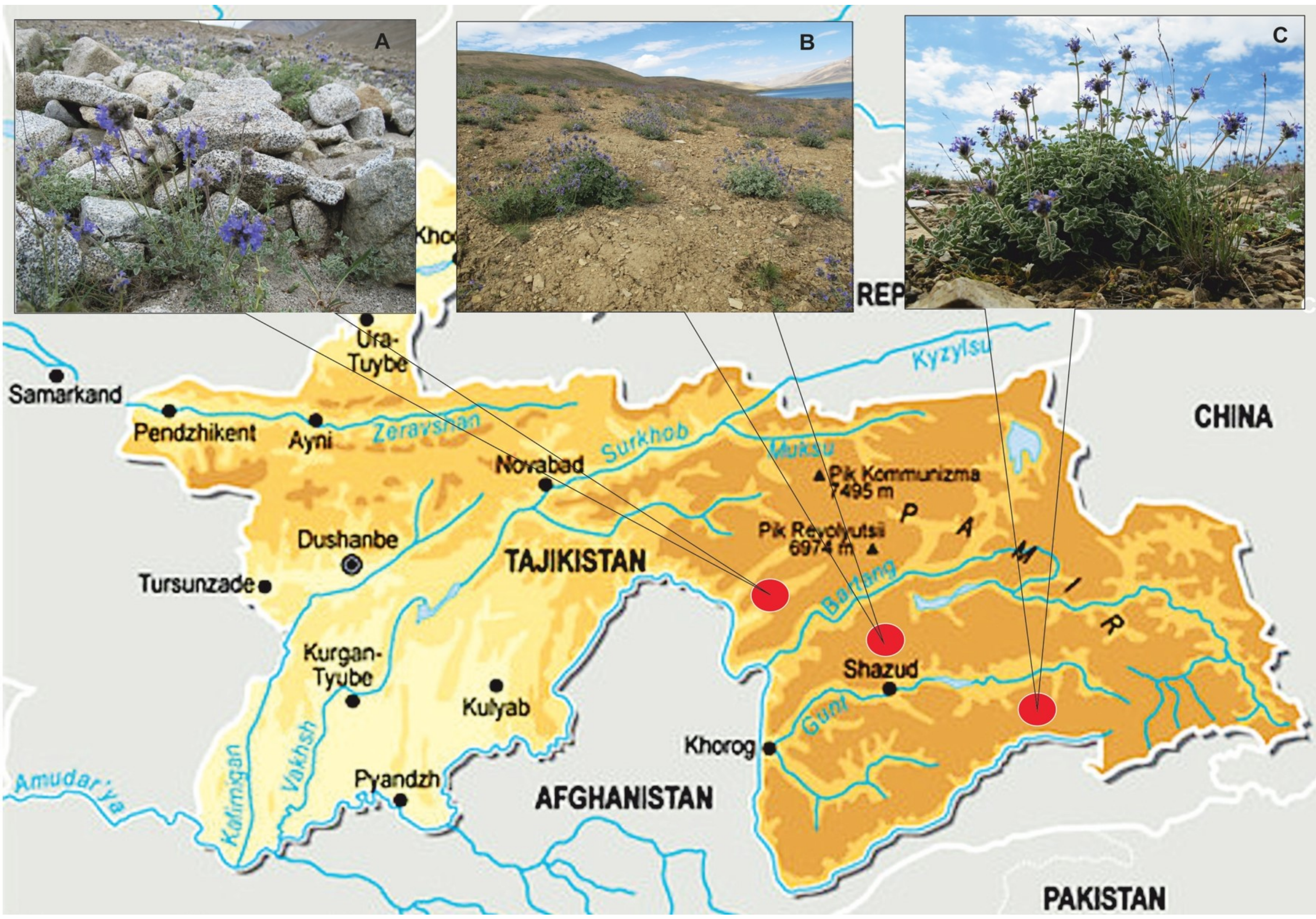

Fig. 1. Location of the sampling sites of *N. pamirensis.* (**A**) population 1, (**B**) population 2, (**C**) population 3 (photo by the authors, map borrowed from the public domain on the Internet).

(Fig. 1): Western Pamir – population 1; 2 Eastern Pamir – population 3.

Research design

The ontogenetic structure of the populations was studied by the generally accepted method (12-14, 18-23). An individual of seed origin was chosen as a counting unit. In populations, the ratio of plants in different ontogenetic states was determined. In total, 750 individuals from different ontogenetic states were studied. To assess the vitality of individuals, 25 plants of the middle-aged ontogenetic state were selected in each population. In these plants, the following characteristics were measured: shoot length, number of generative shoots, inflorescence length, biomass of individuals and potential seed productivity per individual (sp). The duration of ontogenesis was determined by the calendar and biological age of the individuals of different ontogenetic states. The calendar age of each stage was determined by counting caudex growth rings. The rings were counted on an anatomical section using a Carl Zeiss SteREO DiscoveryV12 stereomicroscope with an AxioCam HRc camera (Germany). As the base, 30-150 plots of size 1 m^2 were established, in which all individuals of the species were counted. The transects were located in such a way as to cover the boundaries and the center of the studied populations.

The ontogenetic structure of the populations was studied by the generally accepted method (12-14, 18-23). An individual of seed origin was chosen as a counting unit. In populations, the ratio in plants of different ontogenetic states was determined. Ontogenetic states were determined according to the periodization of ontogenesis (12): seed (1), seedling (2), juvenile (3), immature (4), virginile (5), young generative (6), mature generative (7), old generative (8), subsenile (9) and senile (10). When characterizing the population, classifications were used according to the absolute maximum of ontogenetic groups (12, 13) and “delta-omega” (24). The following indicators were also used in the work:

Population recovery index (Irec) (22):

$$Irec = \frac{\sum_{i=3}^{5} n_i}{\sum_{i=3}^{10} n_i}$$

Population aging index (Iag) (25):

$$Iag = \frac{\sum_{i=9}^{10} n_i}{\sum_{i=3}^{10} n_i}$$

Generative index (Ig) (25):

$$Ig = \frac{\sum_{i=6}^{8} n_i}{\sum_{i=3}^{10} n_i}$$

Efficiency index (ω) (24):

$$\omega = \frac{\sum_i e_i n_i}{N}$$

Age index (Δ) (12):

$$\Delta = \frac{\sum_i m_i n_i}{N}$$

When: e_i – the relative efficiency of energy consumption by individuals of the *i*-th ontogenetic state, m_i – the age of individuals of the *i*-th ontogenetic state, n_i – absolute number of individuals of *i*-state, *N* – the total number of individuals in the coenopopulation, 3–10 – number of ontogenetic states.

The indicator of ecological density was given according to standard procedure (26). The determination of the ontogenetic state of *N. pamirensis* individuals was based on the ontogenesis previously studied by us (17).

Statistical analysis

The quantitative indices analysis of individuals was performed using STATISTICA 10.0 and Microsoft Excel 2010 (Microsoft, USA). The data were represented as mean ± standard deviation. The correlation was analysed using Pearson’s correlation coefficient ($p < 0.05$ to $p < 0.001$; n = 75). The Kruskal-Wallis test was used to determine the significance of morphological interpopulation variability. Spearman's rank correlation coefficient was used (n = 150; $p < 0.05$ to $p < 0.01$) to examine the correlation between the characteristics of individuals (life form type; h: length of the generative shoot (cm); n: number of generative shoots (it.); l: length of the inflorescence (cm); s: number of flowers in individuals (it.), m: biomass of individual (g); sp: seed productivity (ovules per individual) and environmental conditions (stony substrate, projective cover by stones and altitude above sea level) (27). Normality was examined using the Shapiro-Wilk Test (Royston 1982 28).

Results

Three populations of *N. pamirensis* were examined at different heights of the Pamirs. Seed propagation is the main method of replenishment of individuals in populations of *N. pamirensis*; therefore, the generative sphere and the associated basic elements of individuals are one of the key indicators in the analysis of populations.

Table 1. shows the values of some morphological features of *N. pamirensis*. With an increase in the altitude gradient, the morphological characters of *N. pamirensis* changed in the direction of their increase. They reached the highest values at the height of 4250.

Table 1. Biometric indicators of *N. pamirensis* individuals in different habitats

No p	h	n	l	s	m	sp
	M±s	M±s	M±s	M±s	M±s	M±s
1	24.2±3.8	27.2±2.1	1.5±0.1	39.2±1.7	32.4±0.9	2494.8 ±248
2	16.4±2.2	38.9±1.4	1.5±0.1	49.1±1.6	35.2±1.1	3780.4 ±201
3	13.5±1.1	51.2±2.7	1.3±0.1	56.3±1.9	42.7±1.3	10355.2 ±274

No p: population number; **h**: length of the generative shoot (cm); **n**: number of generative shoots (it.); **l** : length of the inflorescence (cm); **s**: number of flowers (it.): **m**: biomass of individual (g); **sp**: potential seed productivity (ovules per individual); **M**: average: **s**: standard error**.**

Of all the selected characters, the length of the generative shoots had a strong inverse relationship with the altitude (r_s = -0.802; p <0.05) and a strong direct relationship with the number of generative shoots (r_s = 0.618; p <0.05). This, in turn, determined a close relationship with the potential seed productivity (r_s = 0.849; p < 0.05). The biomass of the individuals was positively correlated with the type of life form (r_s = 0.456; p < 0.05) and PSP (r_s = 0.849; p < 0.05).

Fig. 2a shows the ontogenetic spectrum of the population examined at h=3060 m a.s.l. (population 1). The location was the valley of the Motraun–Dara River, Yazgulem Range, high-mountain steppe belt (38.103889 N, 71.483861 E) in the bed of a branched stream on a rocky slope of southeastern exposure. The sparse plant aggregation consisted of single specimens of *Potentilla dealbata* Douglas ex Hook., *Carex orbicularis* Boott, *Rosa nanothamnus* Boulenger and a protective cover (PC) of *Nepeta pamirensis* 2%. The total projective cover (TPC) was 7%. The spectrum was complete and included all ontogenetic groups of individuals, multimodal with peaks on juvenile (15%), virginal (18%) and mature generative individuals (26%). Despite the low indicators of potential seed productivity, there were many young plants in the population, which indicated the viability of young plants in the conditions of local moisture.

Fig. 2b shows the ontogenetic spectrum of the population examined at h = 4125 m a.s.l. (population 2). The location was the river Dzhelandy (Alichur Range) high mountain steppe belt (37.546278 N, 72.573972 E). The location was the valley, a large rocky slope of the northwestern exposure. The plant aggregation consisted of *Ziziphora pamiroalaica* Juz., *Oxytropis immersa* (Baker) Bunge ex Lipsky and *Stipa glareosa* P.A. Smirn. dominated in plant aggregation. The TPC was 15%, and the PC *Nepeta pamirensis* was 3%. The spectrum of the population was monomodal and centered. The absolute peak, as in population 1, fell on mature generative individuals (28%). However, in population 2, there were very few young plants (juvenile: 8%, immature: 7% and virginal: 10%), which indicated poor replenishment of the population with seeds and many old generative ones, which indicated a long development of plants in the generative period. Fig. 2c shows the ontogenetic spectrum of the population examined at h=4250 m a.s.l. m. The location was the valley of an alpine plateau on the endorheic lake terrace of Lake Turumtai-Kul, Alichur Range, pillow belt (37.468194 N, 72.560889 E (population 3). The shores of the lake are composed of clay soil covered with small pebbles (30%). *Nepeta pamirensis* (PC 8%) prevailed in the plant aggregation on the leveled slightly sloping section of the terrace. The TPC did not exceed 20%. *Poa tianschanica* (Regel) Hack. ex O. Fedtsch. (8%) dominated in herbage. The spectrum was different from all the others. It was bimodal, with peaks on juvenile (31%) and mature generative (23%) individuals; there were also many old generative individuals in the population. Under these conditions, the seed productivity was the largest (Table 1), but the low proportion of other young plants (immature: 6% and virginal: 4%) indicated their high elimination and low viability in conditions of the increased dryness of the climate. This type of spectrum was temporary and reflected a new wave of population development. Table 2 shows the distribution of *N. pamirensis* in different populations. In general, individuals were distributed in sparse groups.

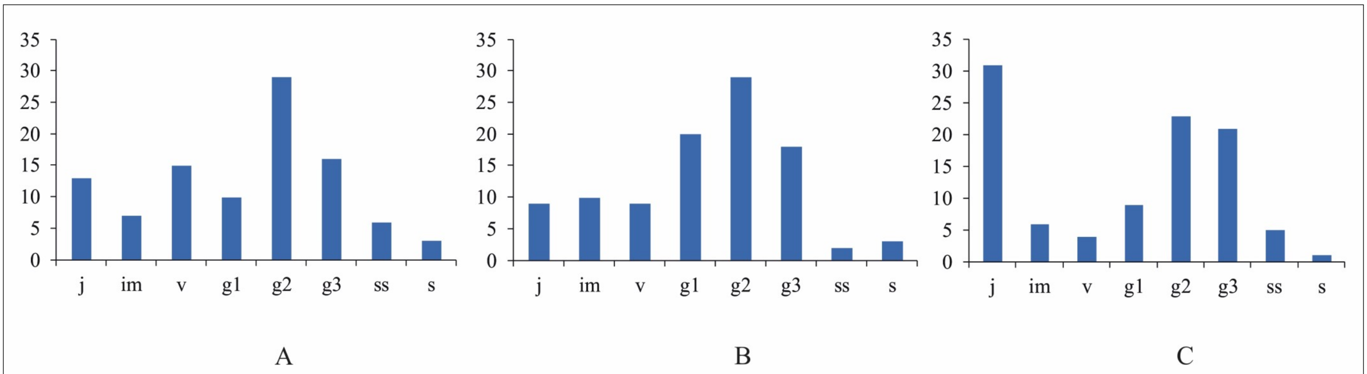

Fig. 2. Ontogenetic spectrum of *N. pamirensis* population of the Pamirs. (**A**) spectrum population 1, (**B**) spectrum population 2. (**C**) spectrum population 3. Ontogenetic groups: (**j**) juvenile, (**im**) immature, (**v**) virginile, (**g1**) young generative, (**g2**) mature generative, (**g3**) old generative, (**ss**) subsenile, (**s**) senile (compiled by

Table 2. Spatial distribution of *N. pamirensis* individuals in different habitats of the Pamirs

No p	Habitat	Ecological population size, m²	Population size, m²		
			min	M±s	max
1	Along the riverbed	4.3	1	1.5±0.57	8
2	Rocky slope	6.2	1	1.7±0.78	17
3	Intermountain valley	8.3	1	2.1±1.10	25

No p: population number; **M**: average; **s**: standard error; **min**: minimum feature value; **max**: maximum feature value.

In population 1, individuals were unevenly distributed along the riverbed. The population size was from 1 to 8 ind./m², and the average ecological density was 4.3 ind./m². In population 2, the population size varied widely from 1 to 17 ind./m². In contrast to population 1, the average ecological density in the population 2 was 1.4 times higher (6.2 ind./m²). In population 3, the population size was much higher than in other populations; it ranged from 1 to 25 ind./m². The average ecological density was also the highest (8.3 ind./m²). The demographics of the populations are presented in Table 3. In population 1, the recovery index was increased (Irec = 0.72), which indicated a good replenishment of the population with seeds. The generativity index was average (Ig = 0.48), it was formed mainly due to the mature generative plants. The proportions of old generative plants and those in the post-generative period were insignificant, which indicated the rapid rate of ageing and death of individuals. This led to a low population ageing index (Iag = 0.06). The indices of age (Δ) 0.39 and efficiency (ω) 0.61 characterized the population as transitional to the mature type.

Table 3. Demographics of populations *N. pamirensis* individuals of the Pamirs

No p	Irec	Ig	Iag	Δ	ω
1	0.72	0.48	0.06	0.39	0.61
2	0.34	0.69	0.08	0.44	0.67
3	0.75	0.53	0.03	0.36	0.54

No p: population number; **Irec**: recovery index; **Ig**: generativity index; **Iag**:

The population 2 demographics were different. Despite the increase in seed productivity, the recovery index in this population was low (Irec = 0.34). In general, the generativity index was higher than in population 1 (Ig = 0.69), it was formed due to a large number of mature generative and old generative individuals. In contrast to population 1, population 2 contained a large proportion of old generative plants (23%), which was due to the long ontogeny of this condition. The ageing index was also higher (Iag = 0.08). The indices of age (Δ) 0.44 and efficiency (ω) 0.67 characterized the population as transitional to the mature type too. The demographics of population 3 differed significantly from the other populations. The generativity and recovery indices were the highest (Ig = 0.53, Irec = 0.75), and the main contribution was made by individuals of the mature and old generative states; it indicated a very increased ontogeny of these ontogenetic states. After a long generative period, plants instantly die off; therefore, the ageing index was the lowest (Iag 0.03). The values of the indices of age (Δ=0.36) and efficiency (ω=0.54) characterized the population in the transition towards the mature type.

Discussion

Scientists have looked at how plants adapt to harsh growing conditions by looking at how their life forms and physical traits change along an elevation gradient in different mountainous areas (29–34). It is usually included in various associations and often forms monodominant plant aggregations in sheep's fescue and tragacanth steppes (15). There is no data on the biology of this species in the literature. We previously studied the ontogenesis and different life forms of *N. pamirensis* in different parts of the range (17). In population 1, where *N. pamirensis* is an herbaceous plant, the values of the main morphological characters were the lowest (only the length of shoots was maximum but with a minimum number of generative shoots). The herbaceous life form of *N. pamirensis* and the maintenance of underground renewal buds ensure the viability of the species under such conditions. Higher in the vertical gradient, where *N. pamirensis* is a dwarf semi-shrub (population 2), the values of the morphological characters increased; they reached their maximum values at the highest distribution point (only the length of the shoots was minimal), where *N. pamirensis* forms a dwarf semishrub with a cushion-like growth form (population 3). Partial lignification of the shoots and intensive branching in the aerial part, which leads to an increase in the number of generative shoots, ensure the best adaptation of the species.

Works on the biology of alpine plants indicate that with an increase in the altitudinal gradient, in some species, the duration of the ontogeny increases (33-37). The main factors causing the inhibition of plants are a low temperature, emerging winds, and the increased dryness of the air and soil (38-40). The same pattern was established for *N. pamirensis.* With an increase in the height, the duration of the ontogeny increased. At the lowest altitude, the life span of individuals did not exceed 14-17 years; at the highest point of the survey, the ontogeny was the longest (more than 25 years) (17).

It is known that changes in the life form and the main morphological features under changing external conditions affect the structure of populations (13, 33, 34). Many researchers believe that the centered type of spectrum is an indicator of the wellbeing of the population of many plants with seed reproduction (12, 13, 19, 20). In general, all the surveyed populations of *N. pamirensis*, due to the large proportion of mature generative plants, were attributed to the centered type, but the spectra differed. In population 1, the spectrum was multimodal. The left part of the spectrum had sharp rises and falls in different groups of young plants. This was due to the irregularity of the seed replenishment, which is regulated by the seed productivity. According to some data, in alpine plants, the fruiting phase very often falls out, and the replenishment of populations with seeds occurs extremely rarely (2, 34, 35). Local moisture near the riverbank favorably affects the germination of a small number of seeds but at the same time leads to their washout and a reduction in the lifespan of old individuals. In population 2, examined on a rocky slope, the proportion of young plants was low, which was most likely due to the blowing of seeds from the surface of the substrate. In this population, the proportion of old generative plants increased, which indicated insignificant changes towards the ageing of the population. The accumulation of old generative plants is associated with an increase in life expectancy and the slow ageing of plants. This phenomenon is consistent with studies that show that slow aging rates under harsh conditions are characteristic of high-mountain and arctic plants (37, 40-42). At the highest point of the survey (population 3), the spectrum was bimodal with a predominance of juveniles and a large proportion of mature and old generative of individuals. On the one hand, this was due to the significant seed replenishment of the population; on the other hand, it is also due to the duration of the ontogeny increases in plants and their slow aging. At the same time, the intermountain valley in which the population is located is protected from strong winds. A sharp decline in the population of other young plants (immature and virginal) was associated with their natural elimination.

The sources repeatedly emphasise that strong winds and river floods, on the one hand, reduce the population size and on the other hand, increase the radius between aggregations and contribute to the spread of the species (43, 44). Mountain slopes and riverbanks reduce the population size and density of aggregations in *N. pamirensis* populations. The largest population size and abundance of *N. pamirensis* may be protected from winds in the intermountain valley (populations 3). Usually, in such conditions, plants group next to long-lived adult bushes, which additionally protect young plants. The population size and density of *N. pamirensis* aggregations decreased on the mountain slope (population 2) and the values were the lowest on the riverbank, which is associated with the washout of plants (population 1).

Conclusion

Depending on the altitude gradient, the species was characterised by different efficiencies of seed reproduction, which determined the different densities of individuals in plant communities of distribution. The greatest density and population size of *N. pamirensis* form at the highest altitude of the distribution in the intermountain valley, where they are protected from the effects of strong winds. The ontogenetic structure of the population indicates that on the smallest altitudinal distribution gradient, where *N. pamirensis* has an herbaceous life form, the population is less stable than on the highest gradient, where it forms a dwarf semishrub with a cushion-like growth form. In type, the spectrum of all populations was centred and complete, but with different variants. With an increase in the altitude gradient, differences in the spectra occur in the pregenerative and generative groups due to an increase in seed productivity and the duration of ontogenesis in the mature and old generative states.

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Authors contributions

Conceptualization, AA and VC; methodology, AA and VC; data acquisition and analysis, AA and VC; writing–original draft preparation AA and VC; writing–review and editing, AA and VC; Software, MT; Formal analysis, MT. All authors have read and agreed to the published version of the manuscript.

Compliance with ethical standards

Conflict of interest: The authors declare no conflict of interest.

Ethical issues: None.

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