PLANT SCIENCE TODAY
Vol XX(1): 1-XX
https://doi.org/10.14719/pst.13965

eISSN 2348-1900
OPEN ACCESS

Research Article | Agriculture
2026, Volume XX, Issue X, pp. 1-XX

Influence of environmental factors on the functional traits of the rhizome and population structure of *Nepeta sibirica* L. (Lamiaceae)

Alexey Yu Astashenkov[1,2], Vladimir N Godin[1], Evgenia B Talovskaya[1,2*], Gulnora R Denisova[1] & Vera A Cheryomushkina[1]

[1]Central Siberian Botanical Garden of the Siberian Branch of the Russian Academy of Sciences, Novosibirsk, Russian Federation
[2]Novosibirsk State University, Novosibirsk, Russian Federation

***Correspondence:** Evgenia B Talovskaya, kolegova_e@mail.ru

Abstract

The aim of the work was to identify the environmental factors affecting changes in the functional characteristics of the rhizome of plants and the structure of their populations. *Nepeta sibirica* L. a perennial herbaceous long-rhizomatous plant, was chosen as the subject of this study. This species is widely distributed in Western and Eastern Siberia, Eastern Kazakhstan and Northern Mongolia and can survive in different habitats (mountain and plain steppes, meadows and disturbed habitats). The morphological features and population structure of the species were analysed statistically. The results showed that in ruderal habitats, active shoot formation results in many rejuvenated ramets, which affects the structure of the populations. In indigenous communities, the presence of stones in the substrate and the degree of disturbance of the community have a statistically significant effect on the development of the rhizome and the structure of the populations. Among all the factors considered, moisture, disturbance of communities, the presence of pebbles and sand, grazing degree, disturbance of substrate and relief have the most significant influence on the ontogenetic composition of populations. The results obtained allow for the evaluation of the relationship between the functional characteristics and populations of other long-rhizomatous plant species and their role in other plant communities.

Keywords: environmental factors; functional traits; long-rhizomatous plant; *Nepeta sibirica*; ontogenetic structure; relationship structure

Received: 03 February 2026. **Accepted:** 30 July 2026. **Available online:** Version 1.0: 03 November 2026.

Cite this article: Astashenkov AY, Godin VN, Talovskaya EB, Denisova GR, Cheryomushkina VA. Influence of environmental factors on the functional traits of the rhizome and population structure of *Nepeta sibirica* L. (Lamiaceae). Plant Science Today. 2026;XX(X):1-XX. https://doi.org/10.14719/pst.13965

1. Introduction

Vegetatively-mobile or clonal plants are a specific group with a pronounced capacity for vegetative renewal and reproduction (1–3). Plants belonging to this group have several significant biological and ecological advantages over other plants. They are characterised by clonal longevity (immortality), the ability to develop neighbouring territories and high anatomical, morphological and physiological plasticity (1–5). Occurring in a wide variety of systematic groups, vegetatively mobile species are very widespread geographically and act as dominants in many plant communities (1, 6).

In modern plant ecology, the study of natural populations is carried out using the analysis of functional traits. Plant functional traits are morphological, ecological and physiological traits that reflect ecological strategies and determine how species respond to environmental factors and influence trophic levels and the properties of the ecosystem (7, 8).

For plants propagating vegetatively, the most functionally significant traits involve structural elements of the rhizome (the length of annual growth and the number of buds on the rhizome, etc.) (2, 7).

Despite numerous studies, clonal plants and their population organisation remain poorly studied, particularly rhizomatous plants (6, 9). To better understand the biology of certain clonal plants, many researchers have focused on the study of bud banks and their activity on the rhizome under changing conditions (10, 11), the population demography (12–16) and the influence of various factors on functional traits and rhizome growth (2, 17–19). It is obvious that the population organisation and dynamics of clonal plants are the result of the birth and death of ramets and the physiological integration of clones influences ramet demography and underlies the differences in the population biology of ramets and genets (6). As a rule, research on populations of clonal plants omits the study age composition, even though this factor that determines the stability and vector of population development (20–23).

This study analyses the intra- and inter-population variability of key traits of plants and populations under different conditions, which will make it possible to determine the degree of the species' well-being in the community. According to some data, under unfavourable conditions, the morphological characteristics of organisms have a high level of variation and strong correlations. On the contrary, in less favourable and critical conditions for existence, traits have a medium and low range of variation and a low degree of correlation (24). This perspective is used in the assessment of not only plants, but also animals (24, 25). For rhizomatous plants, such studies are extremely rare.

In this work, the environmental factors influencing the formation of ramets of different ages and their subsequent development are identified. The results obtained made it possible to evaluate the relationship between the functional traits of the rhizome and the stability of populations. Using a population approach, the role of a widespread species in steppe plant communities was identified. The results have expanded the understanding of the biology of long-rhizome plants in general. *Nepeta sibirica* L. is a perennial herbaceous long-rhizomatous plant. Traditionally, this species has been considered a potential medicinal plant and has exhibited antimicrobial properties in experiments. The species is also a well-known plant used in perfumery and can be used for essential oil production (26, 27). Since the species is widely distributed in western and eastern Siberia, eastern Kazakhstan and northern Mongolia, it can survive in different ecological and coenotic conditions (mountain and plain steppes, meadows and disturbed habitats) (28, 29) and is characterised by high morphological polyvariance. Thus, the study of its functioning in different ecotopes will reveal strategies for its development and help to improve a better understanding of its population behaviour.

The results obtained allow the assessment of the relationship between the functional traits of the rhizome, the stability of populations of long-rhizomatous plant species and their role in plant communities. The aim of the work is to identify the environmental factors affecting changes in the functional traits of the rhizome and the ontogenetic structure of *N. sibirica* populations.

2. Materials and Methods

Biological features of *Nepeta sibirica*

The population of *N. sibirica* is maintained through vegetative reproduction. It is known that the ontogeny of *N. sibirica* is complex. It consists of the ontogeny of the seed individual and the ontogeny of the ramets (30). In their development, plants undergo all ontogenetic states consistently. At the initial stages of the ontogeny, the plant has only a single shoot. In the immature state, an individual is branched and a bush is formed. In the middle stages of the ontogeny in adult plants, because of lateral vegetative overgrowth, a clump is formed from rejuvenated ramets (virginal (V) state). At the end of the generative period, the clump consists of unrejuvenated ramets (subsenile (SS) or senile state), which become old quickly and die off. As a result of the destruction of communications, each ramet separates from the mother individual and develops independently. Rejuvenated ramets repeat the ontogeny of an adult plant.

Research area

The structure of nine *N. sibirica* populations was studied in the south of Siberia (Republic of Khakassia, Russia) (Fig. 1). The vegetation type and ecological conditions of the research sites are described in Table 1. The type of relief (smooth and bumpy) and moisture conditions (dry and moderate) are indicated according to the method described earlier (31). The soil type (ordinary chernozem and leached chernozem) was characterised using the soil map (32). The presence of stones in the substrate was determined (yes and no) and the substrate was characterised as sandy/unsandy.

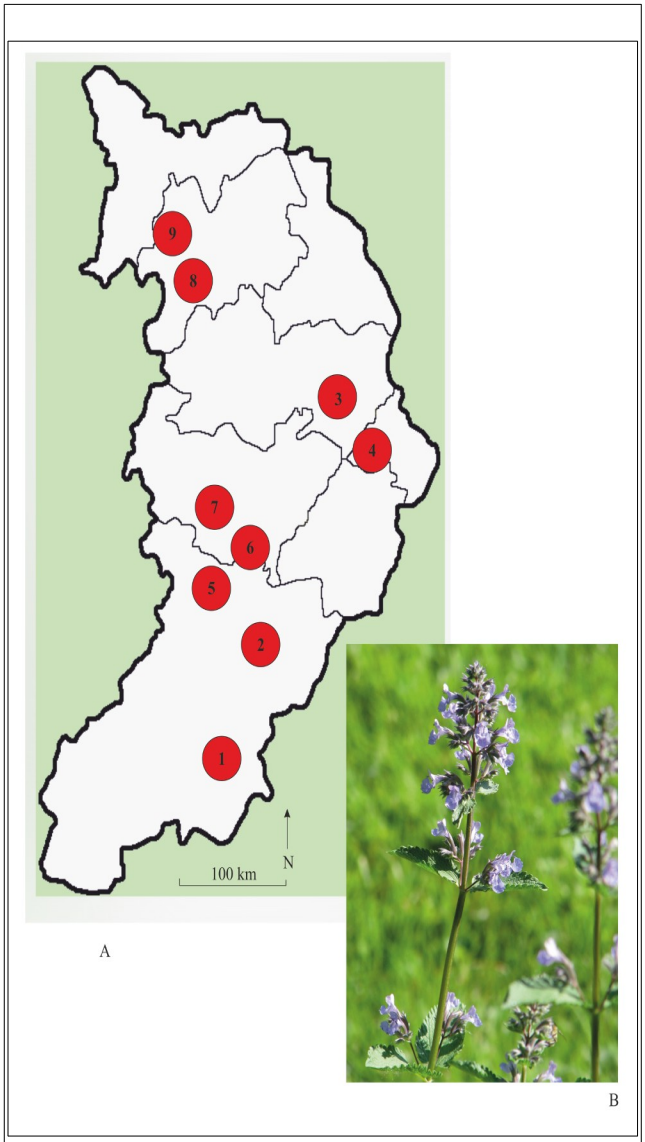


Fig. 1. Locations of *Nepeta sibirica* populations in the Republic of Khakassia, Russia. A: research sites of *N. sibirica* populations; B: flowering plant of *N. sibirica*.

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.
https://doi.org/10.14719/pst.13965

Table 1. Environmental characteristics of *Nepeta sibirica* populations

Sl. No.	Locality	Vegetation type	Environmental factors								
			a	b	c	d	e	f	g	h	j
1	Abaza	Meadow	2	2	2	2	1	2	2	2	1
2	Beltirsky	Meadow steppe	2	1	1	1	2	2	3	2	1
3	Prigorsk	Meadow steppe	2	2	1	1	2	1	3	2	1
4	Tasheba	Meadow steppe	2	2	1	1	1	2	2	2	1
5	Kazanovka	Steppe meadow	2	1	1	2	2	2	2	2	2
6	Kazanovka	Herb bunchgrass steppe	2	1	1	2	1	2	2	1	2
7	Kazanovka	Steppe meadow	1	2	1	1	1	2	1	2	2
8	Malaya Syya	Dry meadow	2	1	1	2	2	1	1	1	2
9	Malaya Syya	Valley meadow	2	2	2	2	2	2	2	2	1

a: relief; 1: flat; 2: bumpy; b: slope; 1: yes; 2: no; c: moisture; 1: dry; 2: moderate; d: soil; 1: ordinary chernozem; 2: leached chernozem; e: stones; 1: yes; 2: no; f: sand; 1: yes; 2: no; g: grazing; 1: weak; 2: moderate; 3: no; h: sodding; 1: yes; 2: no; j: community disturbance; 1: yes, 2: no.

The community's sodding was assessed visually according to the participation of cespitose plants and the presence or absence of sodding was recorded. Plant communities with the participation of *N. sibirica* were considered as ruderal (derived and disturbed) or indigenous (undisturbed). Ruderal communities are understood as a set of species living on disturbed substrates because of anthropogenic impact. Indigenous communities are understood as a set of species composed of historically established phytocenoses as elements of natural flora. The degree of disturbance in the community was assessed according to the participation of weed species (33). The Latin names of the plants were provided according to https://powo.science.kew.org.

Research design

The following rhizome parameters were analysed: rhizome length (Lr), renewal zone length (Lzi), number of buds in the renewal zone (Nb) and rhizome diameter in the middle part (Dr). For statistical analysis, 25–30 individuals from each population were studied. The age and developmental rate of ramets were determined by directly counting annual rings in the perennial part of the rhizome using a Carl Zeiss SteREO Discovery. V12 stereomicroscope with an AxioCam HRc camera (Germany), as well as by counting the preserved geophilic sections of shoots (rhizome modules).

When studying the ontogenetic structure, 10–15 sites of 1 m^2 were laid in each population. A generally accepted methodology was used, based on identifying stages characterised by qualitative features of individual development (20, 34, 35). The following ontogenetic states were identified: seedling (p), juvenile (j), immature (im), v, young generative (g1), mature generative (g2), old generative (g3) and ss. The stages of ontogeny were determined by structural indicators: the presence or absence of embryonic, juvenile or mature morphological characteristics; the ratio of living and dead parts of the plant; and the ability for vegetative reproduction of individuals (21). *Nepeta sibirica* individuals were counted in all ontogenetic states within the boundaries of each site. Thus, the total number of individuals in 9 populations was 2250. Individuals of vegetative origin (ramet) were selected as the counting unit. An indicator of the average ontogenetic spectrum of the population according to the degree of their similarity was used in the study (36). The indicator of similarity between populations was determined using the following equation:

$$r = \sum_{i=1} \sqrt{piqi}$$

Eq. 1

Where, *pi* and *qi* are the frequencies of the *i*-th morph number in the compared populations.

Statistical analysis

Data analysis was carried out using ordinal statistical indicators such as the median of the trait, the standard error of the median, the median coefficient of variation, median asymmetry, kurtosis and the median correlation coefficient (37). According to the median coefficients of variation calculated for each sample, the median value of each trait was determined to obtain a generalised characteristic of the variability of morphological traits in all populations. The ordination of samples from all populations was carried out using the principal component method. Normalised median values of morphological parameters were used for this purpose. The values of the signs were normalised according to Eq. (2):

$$y = (xn - x) / s, \quad \text{Eq. 2}$$

Where, *xn* is the value of the sign, *x* is the median of the sign and *s* is the standard median deviation.

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.
https://doi.org/10.14719/pst.13965

For each sample, a correlation matrix (median correlation coefficients) was calculated, characterising the relationships of all 4 morphological features with each other. To estimate the average level of relationships, the coefficient of determination (the square of the correlation coefficient, r^2) was calculated (38) and averaged across the entire matrix (R^2m) or for individual traits (R^2ch) (Eq. 3 and 4).

$$R^2\mathrm{m} = \frac{\left((r_{12}) \cdot (r_{12}) + (r_{13}) \cdot (r_{13}) + \ldots (r_{nn-1}) \cdot (r_{nn-1})\right)}{(n(n-1) \cdot 0.5)}$$

Eq. 3

$$R^2ch = \frac{\left((r_{12}) \cdot (r_{12}) + (r_{13}) \cdot (r_{13}) + \ldots (r_{nn-1}) \cdot (r_{nn-1})\right)}{(n-1)}$$

Eq. 4

Where, n is the number of analysed features.

To characterise the features of the variability of morphological traits, relative variability (the median of all coefficients of variation for each trait) and consistent variability (the coefficient of determination R^2ch) were further compared. The principal component method was used to identify differences in the structure of the correlation matrices. Before applying this method, the z-transform was performed to approximate the distribution of correlation coefficients to the normal (Eq. (5)):

$$z = 0.5 \cdot ln\left(\frac{1+r}{1-r}\right)$$

Eq. 5

Where, r is the median correlation coefficient.

At the same time, the greater the load of the corresponding matrices on the first main component, the higher the similarity between them. Therefore, the first main component was interpreted as a "factor of generality" (or similarity) of matrices and the corresponding proportion of variance was used as a generalised indicator of the degree of similarity of all compared matrices. The second component reflects the differences between the matrices: high loads correspond to the matrices that differ the most from the rest. The matrices that have high loads with different signs for this component differ the most. The standard Mann–Whitney comparison criterion (U-test, for a pair of samples) was used to compare the obtained values of the median trait values in different populations. The data were processed in the Statistical 10.0 program (Tulsa, OK, USA).

3. Results

Morphological features of *Nepeta sibirica* rhizome

In general, the rhizome of *N. sibirica* is a branched sympodial system from the basal parts of shoots (rhizome modules) with adventitious roots. Because *N. sibirica* shoots can develop from both renewal buds and from dormant buds, the shoots differ in their developmental cycles, which may be monocyclic or dicyclic (Fig. 2).

After the death of the aboveground parts of the shoots, geophilic parts of different lengths are preserved, which are embedded in the general structure of the rhizome. The morphology of the rhizome allows to estimate the age of an individual. The rates of ramet development in different populations were revealed (Table 2). The longest development of the frame was established in ruderal habitats.

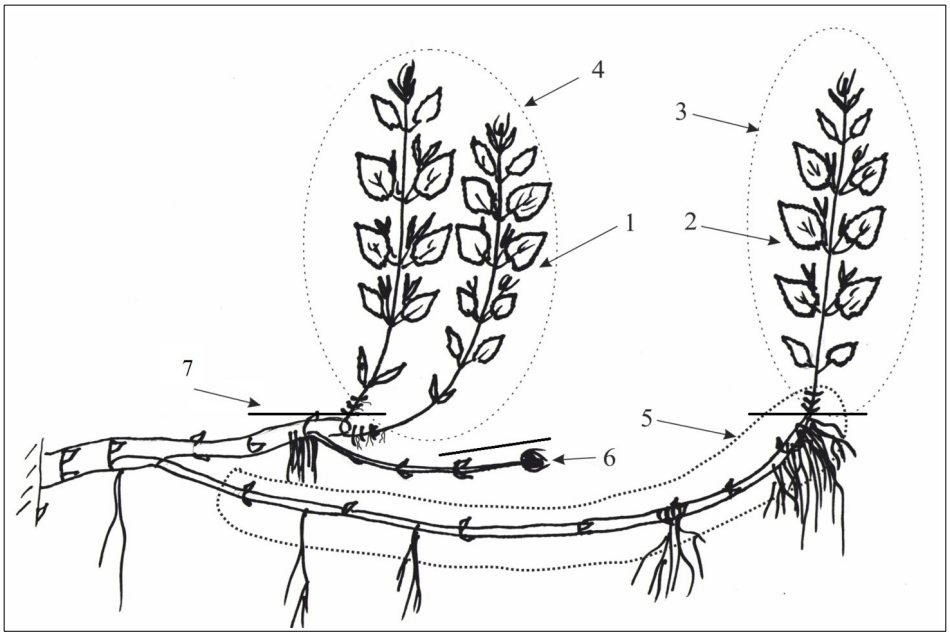


Fig. 2. Aboveground and underground structures of *Nepeta sibirica*. 1: monocyclic shoot; 2: bicyclic shoot; 3: partial shoot (ramet); 4: partial bush (ramet); 5: renewal zone; 6: growing rhizome; 7: substrate level.

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.
https://doi.org/10.14719/pst.13965

Table 2. Rates of development of *Nepeta sibirica* rejuvenated ramets

Habitats	Ontogenetic state							Total, years
	p–j	im	v	g1	g2	g3	ss–s	
Indigenous	–	–	1	1	3	2	2	9
Ruderal	–	–	1	1	2	1	1	6

p: seedling; j: juvenile; im: immature; v: virginal; g1: young generative; g2: mature generative; g3: old generative; ss: subsenile; s: senile.

Ordination of populations according to the morphological features of the rhizome and ontogenetic structure

In all populations, the main part of the variability in the morphological characteristics of the rhizome and the ratio of individuals in different ontogenetic states is included in the first two main components: F1 = 39.8 % and F2 = 27.6 % of the variance (Fig. 3).

According to the first main component, the greatest differences between populations are determined by the degree of habitat disturbance. Ruderal communities have a high proportion of v individuals and a minimal proportion of old (ss and senile) individuals. Individuals of *N. sibirica* have the longest annual growth of the rhizome. Populations studied in indigenous communities exhibit the opposite trend. According to the second main component, the values of F2, the greatest differences are determined by the relief. In communities with bumpy relief, there is a high proportion of middle-aged and g3 individuals. Under such conditions, *N. sibirica* exhibits the maximum length of the rhizome. The opposite is true for populations located in communities with levelled relief, where the length of the rhizome is minimal.

Influence of various factors on the morphological characteristics of the rhizome

The analysis of the influence of ecological and phytocentric factors (relief, slope, moisture, soil type, presence of stones and sand, grazing degree, sodding of the substrate and disturbance) on the morphological parameters of the rhizome in *N. sibirica* individuals is shown in the Fig. 4. Among all the factors considered, three have a statistically significant effect on the parameters of the rhizome: sodding of the substrate, the relief and the disturbance of the community.

It was found that the community disturbance factor affects the morphological features of the rhizome. In disturbed communities, the length of annual growth decreases (U-test = 42625, p-value = 0.009; the influence of the factor is 35.4 % (F-criterion = 7.15, p = 0.03)) and the diameter of the rhizome increases (U = 63531, p = 0.003; 25.1 % (F = 6.98, p = 0.04)).

The decrease in the length of the annual growth is also associated with the factor of sandy substrate (U = 42625, p < 0.001). The influence of this factor is 45.2 % (F = 6.91, p = 0.04). An increase in the length of the communication rhizome is noted in conditions of bumpy relief (U = 63531, p < 0.001; the influence of the factor is 50.5 % (F = 7.13, p = 0.03)).

Correlation structure of functional traits of the rhizome

The analysis of the individual variability of all studied morphological features of the *N. sibirica* rhizome showed that the Lr exhibited average overall and maximum consistent variability (Fig. 5). This parameter refers to the key features that determine the intensity of linear growth and the capture of the territory necessary for the viability of plants.

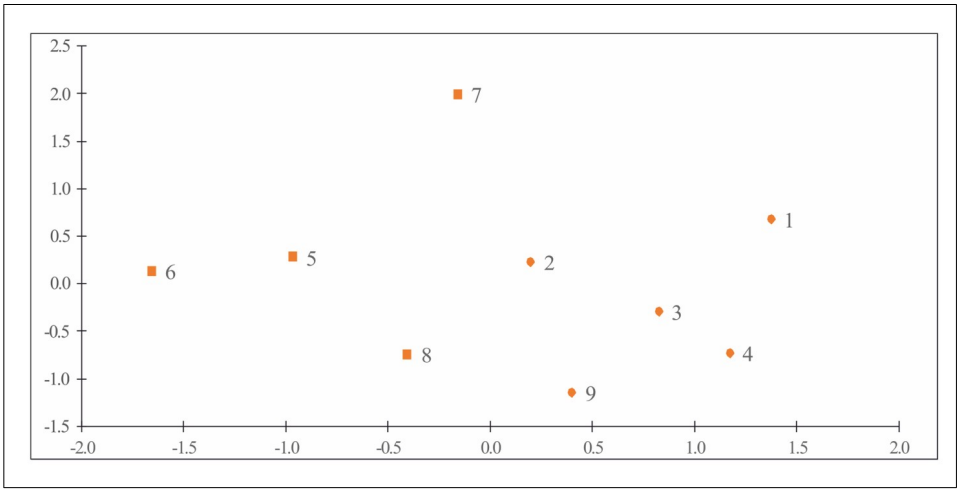


Fig. 3. Ordination of populations in the plane of the first two main components: Morphological characteristics of the rhizome and the ratio of individuals of different ontogenetic states.

1–9: population numbers; circles: ruderal communities; squares: indigenous communities.

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.
https://doi.org/10.14719/pst.13965

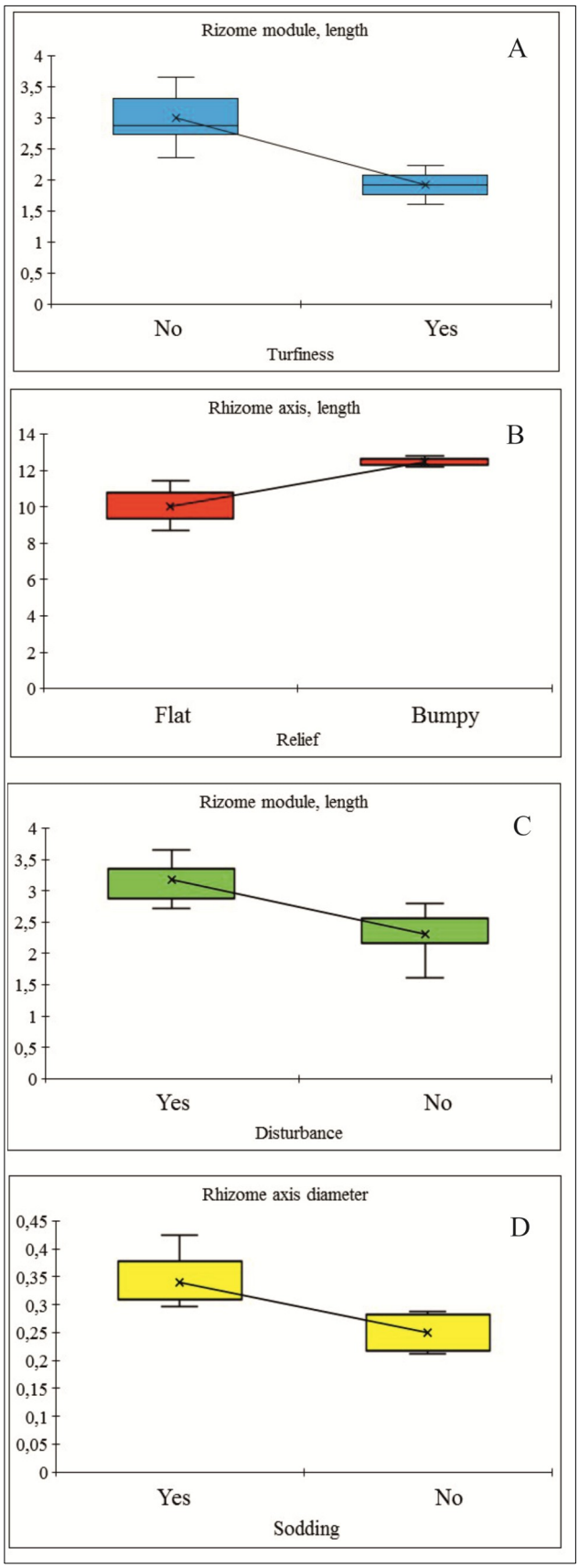


Fig. 4. Influence of factors on rhizome characteristics of *Nepeta sibirica*. The X-axis represents factor gradation and the Y-axis represents characteristic values (cm). A, C: length of annual growth; B: length of rhizome; D: diameter of rhizome.

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.
https://doi.org/10.14719/pst.13965

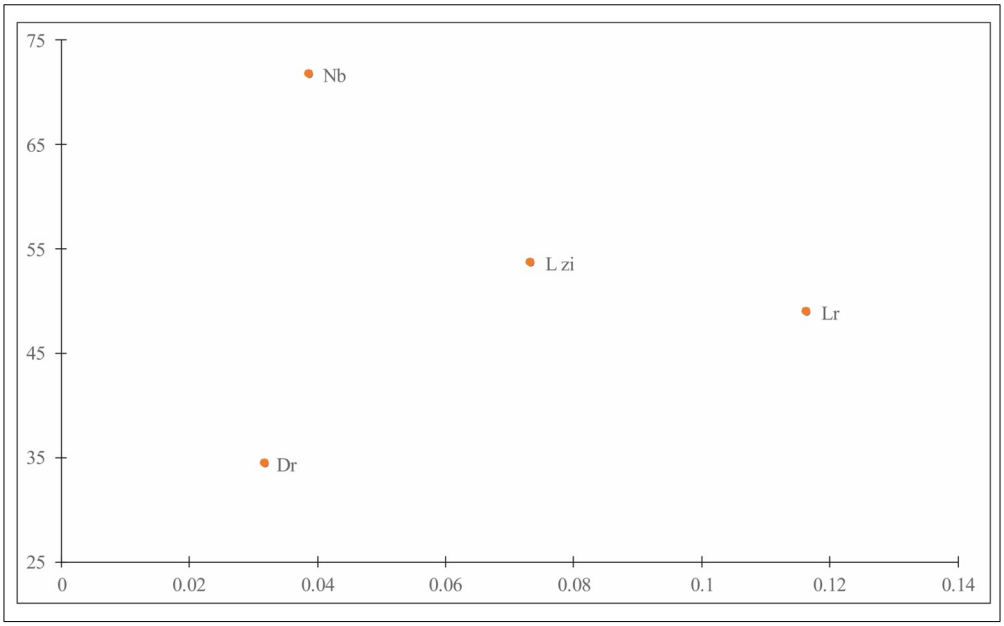


Fig. 5. Structure of variability in the functional traits of the *Nepeta sibirica* rhizome. The X-axis represents relative variability (%) and the Y-axis represents the average determinism of traits. Lr: rhizome length; Lzi: renewal zone length; Nb: number of buds in the renewal zone; Dr: rhizome diameter in the middle part.

The Nb trait has the highest variability and the lowest level of connections with other signs. The variability of this trait is determined mainly by the influence of external factors. However, among the environmental parameters considered, it was not possible to identify which factor determined the value of this feature. Rhizome diameter exhibited the lowest overall and most consistent variability (Fig. 5).

A comparison of the relationship structure revealed an average degree of similarity between the correlation matrices (60.3 %) (Fig. 6). At the same time, the grouping of the matrices clearly shows the correspondence to the types of populations according to the degree of habitat disturbance. This suggests a significant influence of ecological and phytocentric conditions on the consistent variability of morphological features. The matrices of population samples from indigenous habitats are the most similar. The matrix of populations from ruderal habitats differs the most (Fig. 6).

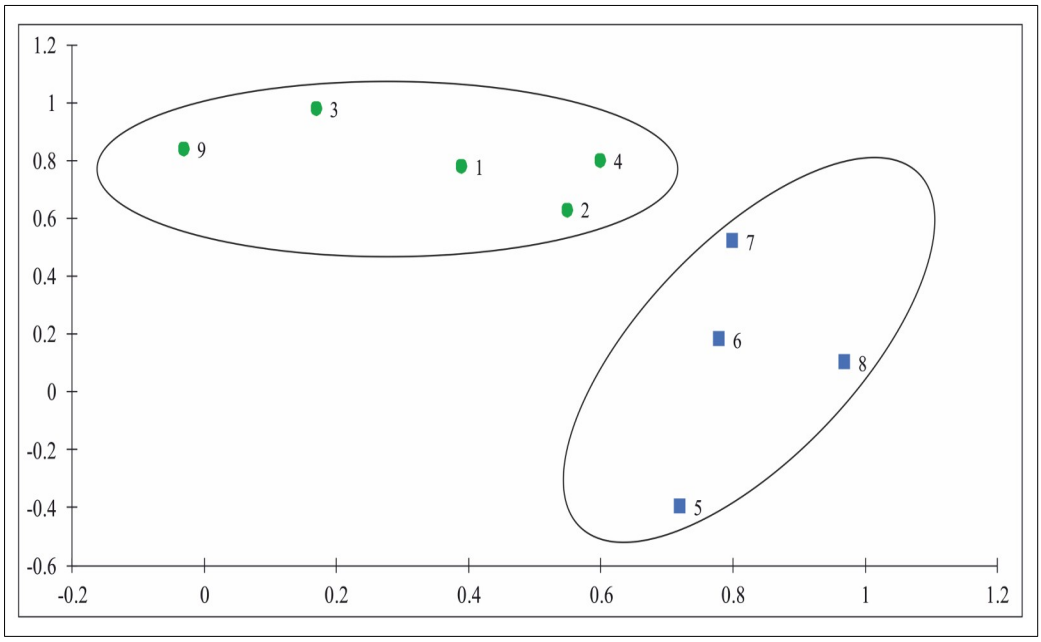


Fig. 6. Ordination of correlation matrices in the plane of the first two principal components. 1–9: numbers of populations; circles: ruderal communities; squares: indigenous communities.

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.
https://doi.org/10.14719/pst.13965

In the conditions of ruderal communities, the relationships among all traits of the rhizome is higher (R^2 = 0.07) than in indigenous communities (R^2 = 0.04).

In indigenous communities, there is a low correlation between the traits (the length of the renewal zone, the length of the rhizome, the number of buds and the diameter of the rhizome). The low consistency of traits at low values is an important adaptive feature of individuals. In these habitats, these indicators are most likely associated with the distribution of resources that are aimed at the maintenance and survival of individuals. Conversely, in ruderal communities, the parameters of the rhizome have high values and there is a high consistency between the traits. Such features occur because, in disturbed habitats, plants invest more resources in intensive rhizome growth for centrifugal expansion and the capture of free space.

Influence of factors on the ontogenetic composition of populations

Among all the factors, moisture, disturbance of the community, the presence of stones in the substrate and relief have a statistically significant effect on the ontogenetic composition of populations.

Under moderate moisture conditions, the maximum proportion of immature individuals was observed in populations, whereas under more arid conditions, the proportion of these individuals was significantly lower (U = 4.19, p = 0.022) (Fig. 7). The influence of this factor was 87.4 % (F = 48.77, p < 0.001).

In populations inhabiting disturbed habitats, the highest proportion of v individuals was recorded, whereas in undisturbed habitats, their proportion was minimal (U = 1.84, p = 0.046). The influence of this factor was 52.1 % (F = 7.60, p = 0.03).

In populations with a stony substrate, the proportion of g1 individuals is significantly lower than in populations without stones (U = 2.00, p = 0.041). This factor determines 45.6 % of the variability of this indicator (F = 5.90, p = 0.04).

In the populations studied in communities with bumpy relief, the proportion of ss individuals was significantly higher than in populations with levelled relief (U = 4.00, p = 0.036). The effect of this factor is 53.7 % (F = 8.10, p = 0.02).

The high content of individuals in the post-generative period (ss and senile plants) in populations with uneven relief where excess moisture accumulates reflects the rapid rates of decay of communication areas of rhizomes; this entails the rapid rates of aging among individuals.

Based on the analysis of the ordination of populations according to the values of the morphological signs of the rhizome, the degree of similarity of the correlation structure (Fig. 6) and the calculation of the similarity index of the ontogenetic structure of the population (r), two groups of populations were identified: populations of disturbed habitats and populations of undisturbed habitats. Based on the high (r) of disturbed (r = 0.89) and undisturbed (r = 0.91) habitats, averaged ontogenetic spectra for each group were constructed (Fig. 8). In undisturbed habitats, the ontogenetic spectrum is bimodal (Fig. 8A) (the first peak falls on g1 individuals (24 %) and, the second peak on ss (21 %)); in disturbed habitats, the spectrum is left-sided (with a maximum on v individuals (44 %) (Fig. 8B).

The bimodal type of spectrum is associated with the formation of many v ramets and slow rates of development in individuals of different ontogenetic states (Table 2). The left–sided spectrum is associated with high vegetative reproduction, rapid rates of development and the aging of individuals.

4. Discussion

It is known that the response of species to the influence of external conditions occurs both at the organismal and population levels and consists of a natural change in the size indicators of morphological characteristics, the ratio of individuals of different ontogenetic states and the density of individuals in populations (25, 39, 40). The main factors determining the morphological structure of individuals and population structure may be the degree of disturbance of the phytocoenosis, the nature of the substrate, the availability of water and organic substances and the phytocoenotic environment (41, 42). Our data indicate that along a gradient from favourable to unfavourable conditions, discoordination (rearrangement) of characters occurs and the amplitude of their variation changes in *N. sibirica* populations. Studies of *N. sibirica* populations under different conditions have shown that in indigenous communities the values and correlations of *N. sibirica* rhizome traits are minimal and such conditions can be considered less favourable for the growth and development of this species. Notably, the results are consistent with Rostova's assumption that there is a connection between living conditions and the correlation of plant traits (24, 25). Reduced moisture, a soddy substrate with stones and levelled relief lead to a decrease in the parameters of the rhizome of *N. sibirica* (the length of the rhizome and the length of the regeneration zone are shortened and the number of buds is reduced). The same response of plants to lack of water, high competition from surrounding vegetation and a decrease in the number of active buds on the rhizome has been described in many other clonal plants. In general, indigenous communities make it difficult to form dicyclic shoots with long geophilic parts. In such habitats, predominantly monocyclic shoots form on the *N. sibirica*. Another main feature is that the rate of ontogenesis of *N. sibirica* individuals slows down and the intensity in the formation of rejuvenated ramets and their peripheral growth decreases. All of this influences the structure of populations in indigenous habitats.

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.
https://doi.org/10.14719/pst.13965

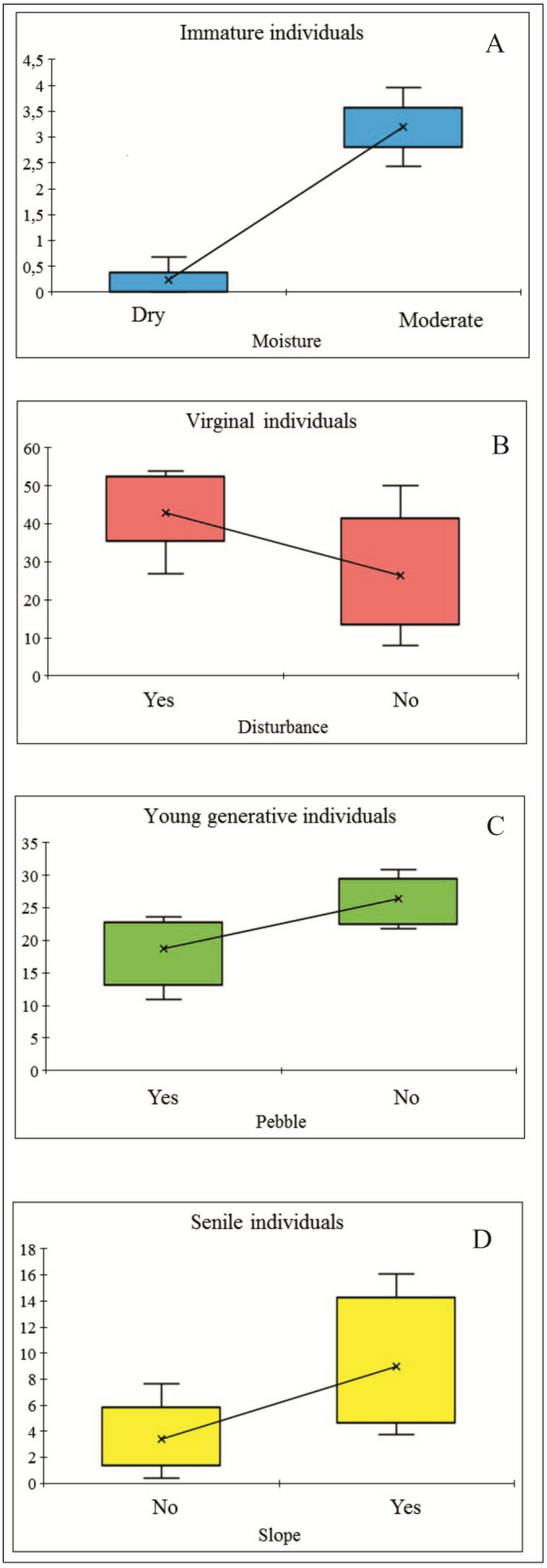


Fig. 7. Influence of various factors on the ontogenetic composition of *Nepeta sibirica* populations. X-axis represents factor levels and Y-axis represents number of individuals per unit area (% of the total number). A: moisture; B: habitat disturbance; C: pebble content; D: slope.

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.
https://doi.org/10.14719/pst.13965

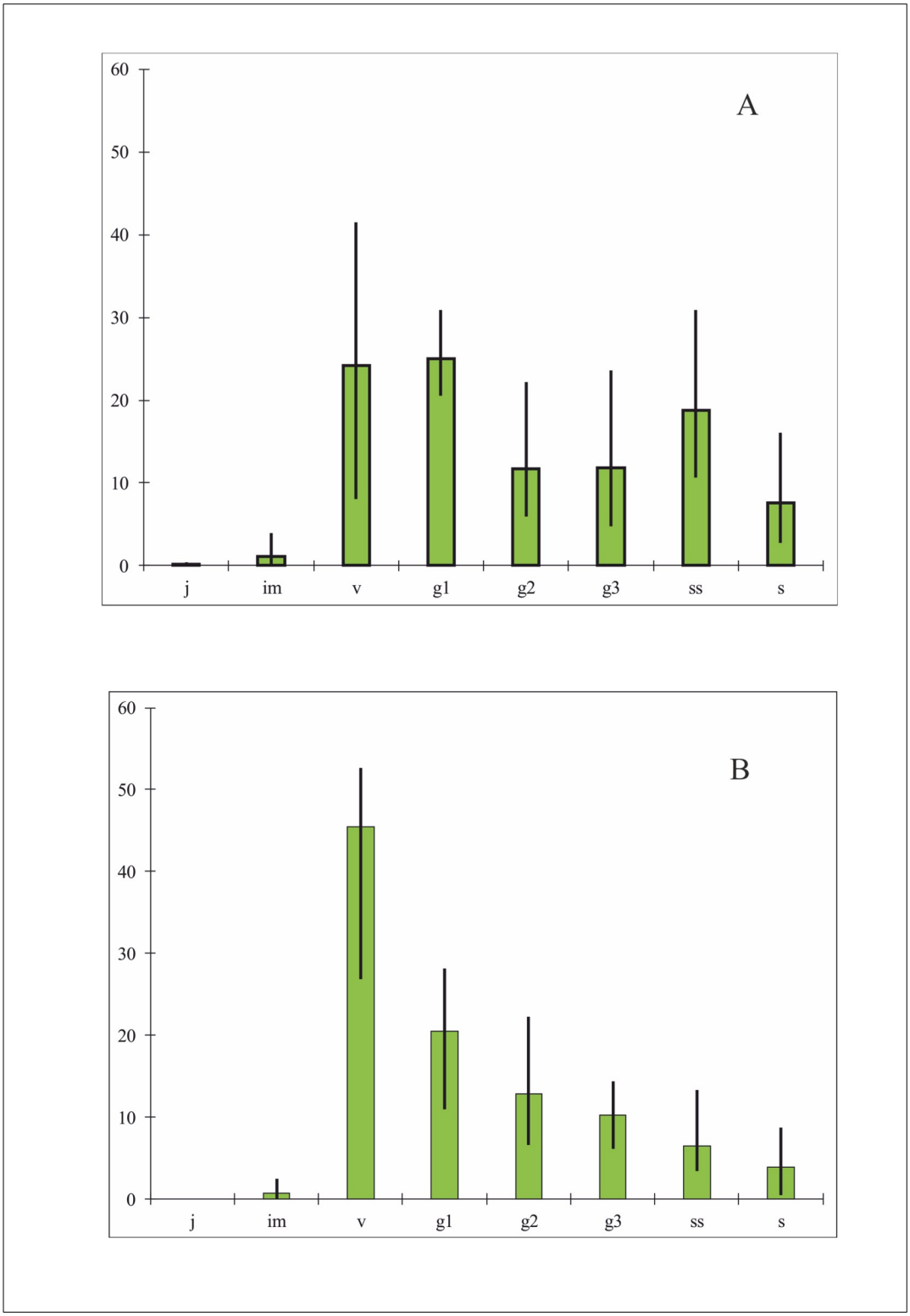


Fig. 8. Averaged ontogenetic spectra of *Nepeta sibirica* populations. X-axis represents ontogenetic groups: p: seedling; j: juvenile; im: immature; v: virginal; g1: young generative; g2: mature generative; g3: old generative; ss: subsenile; s: senile. Y-axis represents number of individuals per unit area, % of the total number. A: undisturbed habitats; B: disturbed habitats.

In native communities, the correlation shift in *N. sibirica* individuals is aimed at the maintenance and survival of individuals. In such conditions, resources are limited and plants cannot afford to spend a lot of energy on growth and reproduction at the same time. Low vegetative reproduction is compensated by the long-term development rates of individuals in the old ontogenetic state. In contrast, in ruderal communities, the correlation shift is aimed at overall scaling. There are abundant environmental resources, plants can afford to allocate resources for growth and intensive vegetative reproduction. *Nepeta sibirica* individuals redistribute resources to benefit of increasing the number of offspring.

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.
https://doi.org/10.14719/pst.13965

Since the ontogenetic spectrum depends on the biological properties of a species (the rate and the pattern of dying off individuals, the rhythm and arrival of germs, the duration of ontogenetic states and others), which can be quantified for each combination of external factors, it becomes possible to calculate the ontogenetic spectrum for specific populations. Thus, ontogenetic composition is one of the essential features of the state of plant populations (20). The position of the absolute peaks of the spectrum reflects the predominance of individuals in a particular ontogenetic state. The left-sided type of spectrum indicates the regular renewal and accumulation of young plants. The bimodal type of spectrum often reflects the uneven renewal and asynchronous rates of development of individuals in a population.

The ontogenetic spectrum of *N. sibirica* populations in indigenous communities is bimodal. The proportion of v individuals in populations is 2.3 times lower than that populations from ruderal habitats, the accumulation of both young and old plants in populations reflects the slow turnover of generations. A similar type of ontogenetic spectrum in undisturbed communities is observed in other plants (*Silene repens* Partin, *Thermopsis lanceolata* R. Br., *Aegopodium podagraria* L.) and is characterised as a sign of a tolerant type of strategy (43, 44).

In ruderal communities with a hummocky, non-soddy substrate and moderate moisture, *N. sibirica* develops a long rhizome with an elongated renewal zone with many buds. Under such conditions, *N. sibirica* development accelerates, the values and correlation of traits are high and the ontogenetic spectrum is left-sided. In some studies, it is noted that intensive overgrowth and an increase in the linear growth of the rhizome occur in the absence of competitive species and on the slopes of mountains (1, 15). In ruderal habitats of *N. sibirica*, active shoot formation and accelerated ontogeny rates lead to the formation of many rejuvenated ramets, which affects the structure of populations. The rapid transition between ontogenetic states reflects the rapid turnover of generations. The literature indicates that a similar spectrum of populations is characteristic of other long-rhizomatous plants in ruderal communities (*Pteridium aquilinum* (L.) Kuhn, *Zerna inermis* (Leyss.) Lindm, *Phlomoides agraria*, *Potentilla bifurca* (Bunge) Adylov, Kamelin & Makhm.) (1, 43, 45, 46) and reflects the reactive type of a population strategy.

The different ratio of individuals in *N. sibirica* populations in different habitats indicates two opposite vectors of their development. In undisturbed habitats, the ontogenetic spectrum indicates that populations are in an unstable state and are approaching aging and possibly even complete extinction of the species from the community. In disturbed habitats, on the contrary, the ontogenetic spectrum indicates a stable state and successful development of populations.

5. Conclusion

The degree of disturbance of communities, the features of the substrate (the presence of stones) and the relief exert a significant influence on the development of the rhizome and the ontogenetic structure of *N. sibirica* populations. In native habitats with flat terrain, reduced moisture and a stony soddy substrate, a rhizome with a short renewal zone develops. The ontogenetic spectrum is bimodal. The viability of populations is regulated by low but regular vegetative reproduction and slow development. In ruderal habitats with a hummocky, non-soddy substrate a rhizome with a long renewal zone develops. The development of individuals accelerates, the values and correlation of traits are maximal and the ontogenetic spectrum is monomodal and left-sided. The viability of populations is regulated by high and regular vegetative reproduction and rapid rates of development of individuals.

Our research can be used to assess biodiversity and protect natural ecosystems at different levels of organisation. The application of the population-ontogenetic approach makes it possible to convincingly predict the development trend of clonal plants and identify the features of the functioning of their natural populations in different environmental conditions.

Our work is the first attempt to analyse the population organisation of clonal herbs through the analysis of functional features. Future research should focus on the analysis of functional traits and the search for their relationships with the structure of populations in other clonal plants. In this regard, not only herbaceous plants are interesting, but also semi-woody and woody plants with a vegetative method of reproduction.

Acknowledgements

This work was carried out within the framework of the state assignment of Ministry of Science and Higher Education of the Russian Federation, project No. FSUS-2024-0024 and state assignment of Central Siberian Botanical Garden of the Siberian Branch of the Russian Academy of Sciences, project No. 126021217212-5.

Authors' contributions

AYA, EBT and VNG contributed to conceptualisation and methodology. AYA and VAC performed validation while VNG conducted formal analysis. AYA, EBT, GRD and VAC conducted the investigation and provided the resources. AYA and VNG performed data curation and visualisation. AYA drafted the manuscript and AYA, EBT, VAC, GRD and VNG contributed to writing, review and editing. AYA and EBT supervised the study while VAC handled project administration and funding acquisition. All authors read and approved the final manuscript.

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.
https://doi.org/10.14719/pst.13965

Compliance with ethical standards

Authors do not have any conflict of interests to declare.

Ethical issues

None

References

1. Lyubarsky EL, Poluyanova VI. Structure of coenopopulations of vegetatively mobile plants. Kazan: Kazan State University Press; 1984.
2. Klimešová J, Martínková J, Pausas JG, de Moraes M Gomes, Herben T, Yufg FH, et al. Handbook of standardized protocols for collecting plant modularity traits. Persp Plant Ecol Evol Syst. 2019;7(5):1553–60. https://doi.org/10.1016/j.ppees.2019.125485
3. Janovský Z, Herben T. Reaching similar goals by different means-Differences in life-history strategies of clonal and non-clonal plants. Persp Plant Ecol Evol Syst. 2020;44:125534. https://doi.org/10.1016/j.ppees.2020.125534
4. Klimešová J, Nobis MP, Herben T. Senescence, ageing and death of the whole plant: Morphological prerequisites and constraints of plant immortality. New Phytol. 2015;206:14–18. https://doi.org/10.1111/nph.13160
5. Roiloa SR, Alpert P, Barreiro R. Differences in physiological integration between invasive and noninvasive introduced clonal species of *Carpobrotus*. J Plant Ecol. 2019;12:972–81. https://doi.org/10.1093/jpe/rtz035
6. Franklin S, Alpert P, Salguero-Gomez R, Janovský Z, Herben T, Klimešová J, et al. Next-gen plant clonal ecology. Persp Plant Ecol Evol Syst. 2021;49:125601. https://doi.org/10.1016/j.ppees.2021.125601
7. Cornelissen JHC, Lavorel S, Garnier E, Díaz S, Buchmann N, Gurvich DE, et al. A handbook of protocols for standardized and easy measurement of plant functional traits worldwide. Austral J Bot. 2003;51(4):335–80. https://doi.org/10.1071/BT02124
8. Karbstein K, Prinz K, Hellwig F, Römermann Ch. Plant intraspecific functional trait variation is related to within-habitat heterogeneity and genetic diversity in *Trifolium montanum* L. Ecol Evol. 2020;10:5015–33. https://doi.org/10.1002/ece3.6255
9. Sebens KP, Thorne BL. Coexistence of clones, clonal diversity, and the effects of disturbance. In: Jackson JBC, Buss LW, Cook RE, editors. Population Biology and Evolution of Clonal Organisms. Yale University Press; 1985. p. 357–98. https://doi.org/10.2307/j.ctt2250w9n.13
10. Klimešová J, Klimeš L. Bud banks and their role in vegetative regeneration-A literature review and proposal for simple classification and assessment. Persp Plant Ecol Evol Syst. 2007;8:115–29. https://doi.org/10.1016/j.ppees.2006.10.002
11. Wu J, Wang Y, Ma Q, Liu Z. Roles of aboveground vegetation, soil properties, and disturbance in determining belowground bud bank in sand dune ecosystems. Environm Experim Bot. 2020;178:104155. https://doi.org/10.1016/j.envexpbot.2020.104155
12. Harper JL. Population biology of plants. Cambridge, MA: Academic Press; 1977.
13. Noble JC, Bell AD, Harper JL. The population biology of plants with clonal growth: I. The morphology and structural demography of *Carex arenaria*. J Ecol. 1979;67(3):983–1008. https://doi.org/10.2307/2259224
14. Zhukova LA. Population life of meadow plants. Yoshkar-Ola: Mari State University; 1995.
15. Cheryomushkina VA. Biology of *Allium* species in Eurasia. Novosibirsk: Nauka; 2004.
16. Janovský Z, Herben T, Klimešová J. Accounting for clonality in comparative plant demography-growth or reproduction? Folia Geob. 2017;52:443–42. https://doi.org/10.1007/s12224-017-9301-4
17. Bell AD, Tomlinson PB. Adaptive architecture in rhizomatous plants. Bot J Linn Soc. 1980;80(2):125–60. https://doi.org/10.1111/j.1095-8339.1980.tb01662.x
18. Chomicki G. Analysis of rhizome morphology of the Zingiberales in Payamino (Ecuador) reveals convergent evolution of two distinct architectural strategies. Acta Bot Gallica Bot Lett. 2013;160:239–54. https://doi.org/10.1080/12538078.2013.830073
19. Wigley BJ, Charles-Dominique T, Hempson GP, Stevens N, TeBeest M, Archibald S, et al. A handbook for the standardised sampling of plant functional traits in disturbance-prone ecosystems, with a focus on open ecosystems. Austral J Bot. 2020;68(8):473–531. https://doi.org/10.1071/BT20048
20. Gatsuk LE, Smirnova OV, Vorontzova LI, Zaugolnova LB, Zhukova LA. Age states of plants of various growth forms, a review. J Ecol. 1980;68(4):675–96. https://doi.org/10.2307/2259429
21. Zhukova LA. Diversity of ontogenetic pathways in plant population. Russ J Ecol. 2001;32(3):151–58. https://doi.org/10.1023/A:1011301909245
22. Smirnova OV, Palenova MM, Komarov AS. Ontogeny of different life forms of plants and specific features of age and spatial structure of their populations. Russ J Dev Biol. 2002;33(1):1–10. https://doi.org/10.1023/A:1013889926529
23. Swenson NG, Worthy SJ, Eubanks D, Iida Y, Monks L, Petprakob K, et al. A reframing of trait-demographic rate analyses for ecology and evolutionary biology. Int J Plant Sci. 2020;181(1):33–43. https://doi.org/10.1086/706189
24. Rostova NS. Correlations: Structure and variability. St. Petersburg: St. Petersburg Univ.; 2002.
25. Astashenkov AYu, Godin VN, Cheryomushkina VA, Talovskaya EB. Analysis of functional traits and the structure of their relationships in coenopopulations of *Panzerina lanata* (Lamiaceae). Bot J. 2022;107(6):544–60.
26. Budantsev AL, Lesiovskaya EE. Wild useful plants of Russia. St. Petersburg: St. Petersburg Chemical and Pharmaceutical Academy; 2001.
27. Süntar I, Nabavi SM, Barreca D, Fischer N, Efferth T. Pharmacological and chemical features of *Nepeta* L. genus: Its importance as a therapeutic agent. Phytother Res. 2018;32:185–98. https://doi.org/10.1002/ptr.5946
28. Poyarkova AI. Family Lamiaceae. In: Shishkin BK, Bobrov EG, editors. Flora of the U.S.S.R. Vol 20. Akad Sci USSR. 1954; p. 286–360.
29. Budantsev AL. Tribe of Nepeteae Benth. Family Lamiaceae Lindl. (systematic, geography, possibility of use) [thesis]. St. Petersburg: Komarov Botanical Institute of the Russian Academy of Sciences; 1993.
30. Vodolazova SV, Cheryomushkina VA, Kolegova EB, Myadelets MA. Ontogenesis, coenopopulation structure, and ecological-coenotic characteristics of *Nepeta sibirica* (Lamiaceae) in Khakassia. Rast Resur. 2010;46(1):3–16.
31. Korolyuk AYu. Ecological optimum of plants in Southern Siberia. Botanical studies of Siberia and Kazakhstan. 2006;12:3–28.
32. Martynov AA. Republic of Khakassia. Soil map. Moscow: Department of M.V. Lomonosov Moscow State University; 2008.

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.

https://doi.org/10.14719/pst.13965

33. Gorchakovsky PL. Anthropogenic transformation and restoration productivity of meadow phytocoenoses. Ekaterinburg: Ekaterinburg; 1999.
34. Rabotnov TA. Dynamics of plant coenotic populations. In: White J, editor. Handbook of Vegetation Science. Vol 3. The Population Structure of Vegetation. The Netherlands: Junk Publishers, Dordrecht; 1985. p. 121–43. https://doi.org/10.1007/978-94-009-5500-4_6
35. Zaugolnova LB, Zhukova LA, Komarov AS, Smirnova OV. Cenopopulations of plants (essays on population biology). Moscow: Nauka; 1988.
36. Zhivotovsky LA. Population similarity measure for polymorphic characters. J Gen Biol. 1979;40(4):587–602.
37. Sachs L. Applied statistics: A handbook of techniques. Springer; 1982. https://doi.org/10.1007/978-1-4684-0123-3
38. Wright S. The theory of path coefficients a reply to Niles's criticism. Genetics. 1923;8(3):239–55. https://doi.org/10.1093/genetics/8.3.239
39. Vorontsova LI, Zaugolnova LB. Population biology of steppe plants. In: White J, editor. Handbook of Vegetation Science. Vol 3. The Population Structure of Vegetation. The Netherlands: Junk Publishers, Dordrecht; 1985. p. 143–78. https://doi.org/10.1007/978-94-009-5500-4_7
40. Hegland SJ, van Leeuwen M, Oostermeijer JGB. Population structure of *Salvia pratensis* in relation to vegetation and management of Dutch dry floodplain grasslands. J App Ecol. 2001;38:1277–89. https://doi.org/10.1046/j.0021-8901.2001.00679.x
41. Rabotnov TA. On coenopopulations of perennial herbaceous plants in natural coenoses. Vegetatio Acta Geobot.1969;19:87–95. https://doi.org/10.1007/BF00259005
42. Bühler C, Schmid B. The influence of management regime and altitude on the population structure of *Succisa pratensis*: Implication for vegetation monitoring. J App Ecol. 2001;38:689–98. https://doi.org/10.1046/j.1365-2664.2001.00640.x
43. Rabotnov TA. Types of plants strategies. Russ J Ecol. 1985;16(3):123–30.
44. Smirnova OV. Eastern European broadleaf forests. Moscow: Nauka; 1994.
45. Shorina NI. Structure of braken-fern brushes in connection with its morphology. In: Serebryakova TI, editor. Life Forms: Structure, Spectra and Evolution. Moscow: Nauka; 1981. p. 213–32.
46. Basargin EA. Ecological-demographic characterization of *Potentilla bifurca* L. coenopopulations. Russ J Ecol. 2007;38:323–26. https://doi.org/10.1134/S1067413607050050

Additional information

Peer review: Publisher thanks the Sectional Editor and anonymous reviewers for their contribution to the peer review of this work.

Reprints & permissions information: Available at https://horizonepublishing.com/journals/index.php/PST/open_access_policy.

Publisher's Note: Horizon e-Publishing Group remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Indexing: See https://horizonepublishing.com/journals/index.php/PST/indexing_abstracting.

Copyright: © The Author(s). This is an open-access article distributed under the Creative Commons Attribution License CC BY 4.0.

Publisher information: Plant Science Today is published by Horizon e-Publishing Group with support from Empirion Publishers Private Limited, Thiruvananthapuram, India.

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.

https://doi.org/10.14719/pst.13965