

Structure of cenopopulations *Clausia aprica* (Stephan) Korn.-Tr. on the border of the area

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Abstract. The aim of this work was to identify and analyze the ontogenetic and spatial structure of steppe plant *Clausia aprica* (Stephan) Korn.-Tr. (Brassicaceae) cenopopulations at the border of distribution. The study of cenopopulations and their habitat conditions was conducted at 2006–2021 in Samara, Volgograd, and Orenburg Oblasts (Russian Federation). For the first time determined the polyvariance of development of individuals, the duration of ontogenetic stages and complete ontogenesis, peculiarities of spatial location and evaluation of running window methods. A table of prohibitions and resolutions of transitions between ontogenetic states was compiled for *C. aprica* ontogenesis. It was found that permissions of transitions between ontogenetic states are 37.8%. In natural cenopopulations, mutual transitions of individuals from one ontogenetic state to another has adaptive significance and determines the dynamics of the ontogenetic structure. At intervals of 6-8 years, a slight increase in the number of *C. aprica* individuals is observed in the populations, which is ensured by the efficiency of seed reproduction. Thus, self-maintenance and self-renewal of species populations is possible in case of low level of anthropogenic impact on vegetation cover of territories.

The natural-territorial complexes of the steppe and forest-steppe zones are characterized by a variety of vegetation and a set of species composing communities, but their current state depends on the impact of anthropogenic factors. Rare representatives of the flora growing at the borders of their distribution are especially vulnerable. Species at the edge of their ranges reflect individual stages of dispersal, or degradation of the communities to which they are confined, which opens up opportunities to study the genesis of modern flora and vegetation. In addition, the ranges of a number of species are indicators of certain climatic and botanical-geographic boundaries.

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Clausia aprica (Stephan) Korn.-Tr. (Brassicaceae) is a perennial herbaceous steppe plant with a range covering the southeast of European Russia, eastern Ukraine, the Caucasus foothills, western and eastern Siberia, Central Asia, and Mongolia [1, 2]. The species is included in the Red Books of 16 subjects of the Russian Federation and one in Ukraine.

The structure of *Clausia aprica* cenopopulations has been insufficiently studied; at present, there are works carried out in the Lipetsk Oblast and the Republic of Yakutia [3, 4]. The aim of this work was to identify and analyze the ontogenetic and spatial structure of *Clausia aprica* cenopopulations at the border of distribution in the Middle and Lower Volga Regions and the Urals. Parameters of cenopopulations of rare species, including *Clausia aprica*, can serve as diagnostic signs to determine the current state of phytocenoses with their participation and natural-territorial complexes as a whole.

In Samara and Orenburg Oblasts, the species is located on the northern and northwestern border of distribution, while in Volgograd Oblast it is found on the southern and southwestern border. It grows as part of rich herb-steppe communities in the upper part of weakly sodded chalky and stony slopes predominantly of eastern and south-eastern exposition. On the territory of Samara Oblast it is also found in thin mountain pine forests. As a rule, it occurs as a solitary specimen or forms loose groups, avoiding heavily sodded areas. The number of individuals in natural populations of the studied region is not high and amounts to 4000 specimens.

The study of structural features of *Clausia aprica* cenopopulations on the territory of Samara Oblast was carried out in 15 geographical locations; in Volgograd and Orenburg Oblasts, 6 and 7 locations were surveyed, respectively.

The study of cenopopulations and their habitat conditions was conducted in the Samara Oblast in 2008–2021, in the Volgograd Oblast in 2006–2021, and in the Orenburg Oblast in 2012–2020. A multidimensional analysis of cenopopulations was applied: regularities of species ontogenesis, spatial, ontogenetic, vitality structure of cenopopulations and their dynamics, efficiency of seed reproduction and self-maintenance of cenopopulations and other parameters were determined. Geobotanical descriptions and analysis of soil conditions were carried out.

For the first time we determined the polyvariance of development of individuals, the duration of ontogenetic stages and complete ontogenesis, peculiarities of spatial location and evaluation of running window methods.

The method of laying test plots (stationary plots) was used in the field studies. The value of the elementary demographic unit of *Clausia aprica* population influenced the choice of site size. An individual was taken as a counting unit in cenopopulation studies. In some works [4], the species is characterized as a long root-stemmed polycarpic with seminiferous dicyclic monocarpic shoots, capable of rejuvenation by root scions to juvenile or immature state. In conditions of Samara Oblast, this process is not observed; individuals reproduce only by seeds, rejuvenation to early ontogenetic states do not occur. In Volgograd and Orenburg Oblasts, formation of rhizome is noted; data on rejuvenation of individuals are absent.

When determining the parameters of the spatial distribution of individuals in cenopopulations, we calculated $K(r)$ of the Ripley function [5, 6]; the calculation results were presented as the function $L(r)-r$, where $L(r)=\sqrt{K(r)/\pi}$ [7]. The estimation of the density of individuals was performed using the moving window method [8] based on kernel functions [9, 10]. The Monte Carlo simulation method [7] was used to assess the significance of the observed deviations $L(r)$ from $LCSR(r)$. The calculations were performed in the R environment (version 4.0.3) using the SPATSTAT package [11].

The sizes and numbers of *Clausia aprica* populations vary in the surveyed sites. The number of individuals in geographic populations in the territory of Samara Oblast varies from 30 to 500 generative individuals. Population sizes range from 30 m² to 600 m².

In the Samara Oblast, the species is registered in the following communities: *Stipa lessingiana* - *Caragana frutex*, *Stipa pulcherrima* - *Aster alpinus*, *Artemisia austriaca* - *Herbae stepposae* - *Agropyron pectinatum* - *Koeleria sclerophylla* - *Stipa capillata* + *Kochia prostrata*, *Artemisia austriaca* - *Koeleria cristata*, *Herbae stepposae* - *Stipa pulcherrima*, *Stipa lessingiana* - *Galatella villosa*, *Festuca valesiaca* - *Galatella villosa*, *Galatella villosa* - *Stipa pennata*, *Festuca valesiaca* - *Koeleria sclerophylla* - *Herbae stepposae*, *Stipa pennata* - *Herbae stepposae*, *Stipa pennata* - *S. pulcherrima*-*Festuca valesiaca*. In the Volgograd Oblast, the species is found in the communities of *Herbae stepposae* - *Stipa pennata* - *Bromopsis riparia* + *Jurinea ledebourii* + *Astragalus albicaulis* + *Teucrium polium* + *Onosma simplicissima* + etc. In the Orenburg Oblast, it is found in communities of *Stipa orientalis* - *Herbae stepposa petrophytica* co *Spiraea hypericifolia*, *Stipa orientalis* - *Herbae stepposa petrophytica* with *Stipa zalesskii*, *Stipa orientalis* - *Herbae stepposa petrophytica*, dominated by *Stipa zalesskii*, *S. capillata* and steppe herbs, *Stipa orientalis* - *Herbae stepposa petrophytica* with *Elytrigia pruinifera*, *Stipa orientalis* - *Herbae stepposa petrophytica*, *Stipa orientalis* - *Herbae stepposa petrophytica* - *Artemisia salsoloides*.

Observations of the polyvariance development of individuals were carried out at four stationary plots. During the work, the main pathways of *Clausia aprica* ontogenesis were identified. Individuals are characterized by the presence of normal and delayed rates of development, breaks in development, rejuvenation (rare), and a period of quasisenility (rare). Experimental data show that the time of passage of ontogenetic periods by individual individuals of *Clausia aprica* is different and depends both on external environmental factors and on the characteristics of the population itself (for example, when the density of turf in the community increases, *Clausia aprica* develops at a slower rate), but most individuals of this species develop at a normal rate.

A table of prohibitions and resolutions of transitions between ontogenetic states was compiled for *Clausia aprica* ontogenesis (Table 1). It was found that permissions of transitions between ontogenetic states are 37.8%. In natural cenopopulations, mutual transitions of individuals from one ontogenetic state to another has adaptive significance and determines the dynamics of the ontogenetic structure.

Table 1. Inhibitions and permissions of transitions between ontogenetic states of *Clausia aprica* (0 – prohibitions, + – permissions, j – s – indices of ontogenetic states)

	Elimination	Resting	j	im	v	g1	g2	g3	ss	s
Elimination	-	-	+	+	+	+	+	+	+	+
Resting	-	-	0	+	+	+	+	+	0	+
j	+	0	+	+	0	0	0	0	0	+
im	+	+	+	+	+	+	0	0	0	+
v	+	+	0	+	+	+	+	+	+	+
g1	+	+	0	+	+	+	+	+	+	+
g2	+	+	0	0	+	+	+	+	+	+

g3	+	+	0	0	+	+	+	+	+	+
ss	+	0	0	0	+	0	0	+	+	+
s	+	0	0	0	0	0	0	0	+	0

The distribution of all studied *Clausia aprica* cenopopulations according to their predominant generative ontogenetic state is presented in Table 2.

The studies have shown that in *Clausia aprica* the number of individuals in the ontogenetic spectra of cenopopulations at the time of the study in virginile and senile periods ($M=1$) is equal in 1.3% of the studied price populations, a slight excess of young plants over aging ($1<M<2$) is noted in 10.8% of cenopopulations, for most populations (87.9%) the number of pregenerative individuals significantly more senile ($M>2$).

Table 2. Ratio of cenopopulations of *Clausia aprica* with predominance of individuals of a certain ontogenetic state

Predominant generative fraction	Number of cenopopulations, %			
	M<1	M=1	1<M<2	M>2
Young (g1)	-	-	3,2	6,7
Mature (g2)	-	-	4,1	66,9
Old (g3)	-	1,3	3,5	14,3

Development of individuals in the pregenerative period and their subsequent transition to the generative state are directly dependent on meteorological conditions. The percentage of transition of seedlings into the immature and virgin states in one vegetation season is determined by the soil temperature regime and the moisture content of the soil and air environments. Drought and, on the contrary, abundant precipitation increase the percentage of death of young plants.

At intervals of 6-8 years, a slight increase in the number of *Clausia aprica* individuals is observed in the populations, which is ensured by the efficiency of seed reproduction. Thus, self-maintenance and self-renewal of species populations is possible in case of low level of anthropogenic impact on vegetation cover of territories.

In *Clausia aprica* ontogenesis, the rate of passage of ontogenetic states by individuals varies and depends on the genetic information of the species and habitat conditions. Transition from seedlings to the immature state occurs rather quickly (usually within 1 vegetation season), the virginia state can be prolonged (up to 1–3 years), and generative individuals last long enough (up to 8-10 years). Senile individuals die off usually during 1 vegetation season. Thus, the complete ontogeny of individuals is from 5 to 15 years (on average, 9 years; maximum in the Samara Oblast is 21 years).

Rejuvenation of a cenopopulation is a long process because the number of emerging seedlings is small, the percentage of elimination of young plants is high, and the transition to more mature stages is extended in time. The type of cenopopulation dynamics is fluctuational.

The spatial structure was studied in detail in three cenopopulations of *Clausia aprica* on the territory of the natural monument "Gora Kopeika" (Samara Oblast): cenopopulation 1 is exposed to grazing, CP 2 – under normal conditions with low anthropogenic impact, CP 3 – after steppe fire. The obtained results are presented in Figures 1–5.

Analysis of Ripley's function showed that a random type of spatial structure was observed on all the studied sites (Figs. 1–5). In the undisturbed area, there was a slight tendency to repel plants at a distance of 0.2 m (Fig. 5). Density ranged from 1–4 individuals/m² (Fig. 3). Individuals in the middle-age generative state (g_2) dominated, 19 individuals; Repulsion was observed in adult individuals as a result of intraspecific competition, while young plants were mostly confined to maternal organisms (Fig. 3). After the fire, the density was 2–4 individuals/m² (Fig. 1). In the age spectrum, the maximum came to immature individuals (im) – 26 individuals, the second in number was the virginile group (v) – 13 individuals. The Ripley's function plot shows a slight grouping tendency, which is due to the accumulation of pregenerative individuals in adult plants (Fig. 4). Community recovery was probably occurring at this site due to seed germination from the rare remaining generative individuals. Maximum grazing density was 2 individuals/m² (Fig. 2). Total abundance was only 30 individuals. The predominant age states were middle-aged (g_2) with 9 individuals and old generative (g_3) with 8 individuals. Probably, pregenerative age states were of the greatest interest for cattle as fodder.

The state of many known populations of *Clausia aprica* can be characterized as unsatisfactory due to the long-term use of natural-territorial complexes of the Samara Oblast as pastures and recreational facilities.

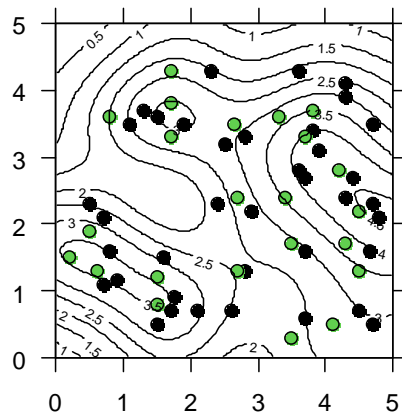


Fig. 1. Map of local density of individuals in a community after a fire (green circles – generative individuals, black circles – pregenerative individuals)

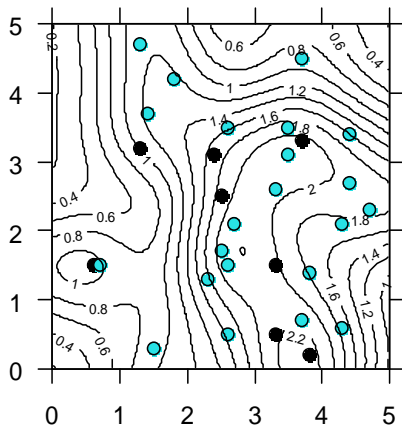


Fig. 2. Map of local density of individuals in the community after grazing (blue circles – generative individuals, black circles – pregenerative individuals)

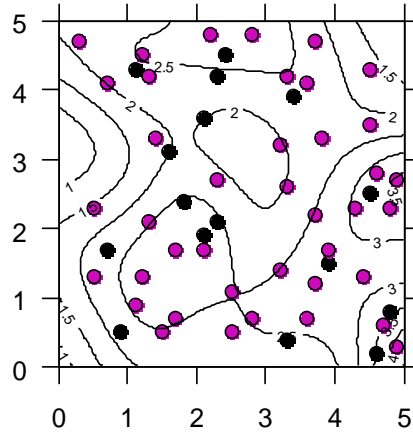


Fig. 3. Map of local density of individuals in an undisturbed community (pink circles – generative individuals, black circles – pregenerative individuals)

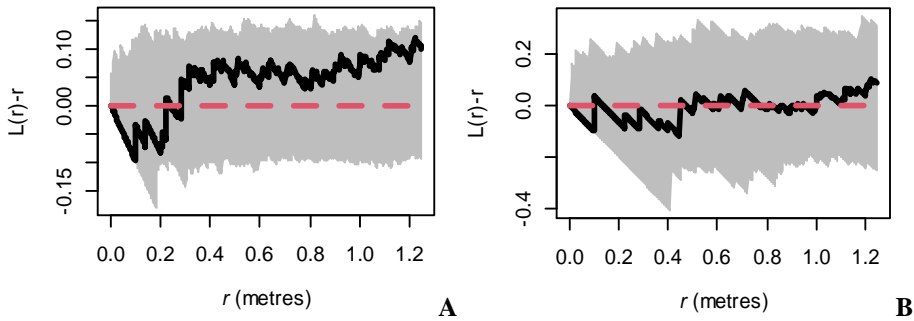


Fig. 4. Behavior of the Ripley function in the community: **A)** after a fire, **B)** after grazing

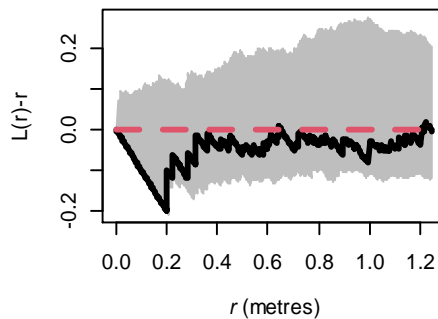


Fig. 5. Behavior of the Ripley function in the undisturbed community

The study of the population dynamics in some populations was carried out. For example, in the right bank of the Buzuluk River (the tract "Mamina Gora") in the vicinity of the farm Pomalinsky (Volgograd Oblast) in two cenopopulations since 2006 the number of individuals was revealed, at first their growth (in 2008 and 2012), and then a sharp decrease was noted.

The recorded increase in the number of individuals in the studied population of *Claudia aprica* after disturbance of natural habitat under the influence of anthropogenic factor (in this case - plowing for forest plantations) is not surprising. Under the conditions of the Volgograd Oblast, the same effect of "rejuvenation" and increase in the number of

individuals of the pregenerative fraction of the population as a result of anthropogenic disturbance of the soil and vegetation cover was also observed in some other species of petrophyton and halophyton studied in detail in cenopopulation respect, located in the region at the border of their cenoareal.

Practical value of cenopopulation studies of *Clausia aprica*, which is a stenobiont, consists in the development of effective ways to assess the degree of conservation of plant communities. The results of the research can be used in the examination of natural-territorial complexes, including specially protected natural areas.

For *Clausia aprica* under optimal ecological and phytocenotic conditions, normal complete cenopopulations with a peak in the mature generative fraction are typical, indicating high ecological plasticity. In definitive populations, the number of individuals and their ratio by ontogenetic periods is constant. In favorable years, the number of seedlings increases. But soon the number of individuals approaches the initial one due to elimination (first of all, pregenerative individuals). Regressive cenopopulations are characterized by low numbers and their gradual or sharp decrease.

The random type of placement of individuals on stationary plots is indicative of favorable habitat conditions for the species. Probably, the degree of influence of anthropogenic factors considered in the work was insignificant and did not lead to transformation of phytocenoses. Thus, there was no loss of any age group on disturbed sites compared to the community under undisturbed conditions; the density of individuals also changed insignificantly. Analysis of the obtained data showed that in the studied communities there is a potential for recovery of the species' cenopopulations due to the pregenerative group of individuals. Random distribution of individuals in small populations indicates their unstable position in phytocenoses.

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