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THE EFFECT OF POPULATION PSEUDO-REJUVENATION IN ADVERSE CHANGES IN LIVING CONDITIONS: A CASE STUDY ON THE HIGHLAND PLANT SPECIES IN THE UKRAINIAN CARPATHIANS

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Abstract

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"Rejuvenation of population" is commonly considered as an increase in the proportion of young individuals in the population. In our opinion, the term "rejuvenation" has to be used in case of an increasing percentage of young individuals providing maintenance or increase of the entire population size. In return, an increasing percentage of young individuals while reducing the number of the entire population should be considered as "pseudo-rejuvenation." A key feature of rejuvenation is the positive dynamics of the population. Instead, pseudo-rejuvenation is an indicator of negative exogenous or endogenous changes and is evidence of population degradation under adverse environment conditions. The article presents the most common examples of the processes of rejuvenation of populations in different plant species under the influence of anthropogenic and natural factors in the plant communities of the Ukrainian Carpathians. The main causes of rejuvenation and pseudo-rejuvenation of populations of the target plant species have been identified. Studies of population structure changes *in situ* were performed using both long-term monitoring transects laid 5–40 years ago and in new sites. Transects are located in the alpine, subalpine, and upper forest zones of the Ukrainian Carpathians in the height range of 1200–2000 m a.s.l. The study areas cover the most common alpine and chionophilic communities, some forest and subalpine phytocenoses.

Key words: age composition, rejuvenation, demography, endangered species.

Introduction

Analysis of the obtained data concerning the ontogeny (Jongejans, De Kroon, 2005), demography (Maschinski et al., 2006; Colas et al., 2008; Cursach et al., 2013; Garnier et al., 2018; Kobiv, 2018; Palaj, Kollár, 2019), age structure (Wang et al., 2004; Dang et al., 2010; Chu, Adler, 2013), and population viability (Bissels et al., 2004; Dhar et al., 2008; Zeigler et al., 2013; Roeder et al., 2019) of endangered species is needed to elaborate effective methods for their conservation and restoration.

In the demography of plants "rejuvenation", as a rule, means an increasing percentage of young individuals in a population and can be considered a positive process. However, populations may fall into the category of rejuvenated, regardless of the changes in their demography as a whole. In fact, reduction in the average age may be the result of the negative impact of different external factors.

In our opinion, the term "rejuvenation" has to be used in case of an increasing percentage of young individuals provided maintenance or increase of the entire population size. Furthermore, increasing the percentage of young individuals while reducing the number of individuals in a population should be considered as "pseudo-rejuvenation".

The concept of "pseudo-rejuvenation of population" was earlier applied for some cases for the purpose of analysis of changes in the age composition and abundance of populations of rare plant species in the highlands of the Carpathians (Kyyak, 2013).

The aim of this article is to summarize the study results of the effects of pseudo-rejuvenation of population due to unfavorable changes in the conditions of its existence, taking the example of plants species in the Carpathian Mountains.

Material and methods

The issue of rejuvenation of plant populations was studied taking the example of several rare species distributed in the highlands of the Ukrainian Carpathians and included in the Red Data Book of Ukraine (Didukh, 2009), which were as follows: *Gentiana acaulis* L., *Leontopodium alpinum* Cass., *Ranunculus thora* L., and *Saussurea alpina* (L.) DC. Comparative studies also included some trivial species that are convenient model objects, which were *Carex curvula* All. and *Heracleum carpaticum* Porc. The selected species are under the influence of various natural changes or human impact and reflect a variety of biomorphological types (growth forms), different ecology, conservation status, and participation in coenoses.

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Studies of population structure changes *in situ* were performed using both long-term monitoring transects laid 5–40 years ago and newly laid research plots. The transects are located in the alpine, subalpine, and upper forest zones of the Ukrainian Carpathians in the height range of 1200–2000 m a.s.l. The study areas comprise the most common alpine phytocenoses, chionophilic, and some forest and subalpine communities, which differ both in ecological–coenotic characteristics and in the degree of anthropogenic transformation due to trampling, grazing, and protection. Most of the transects are concentrated in the central part of the Chornohora Ridge. The altitude of the habitats above sea level, aspect and steepness of the slopes, air temperature, wind and snow regimes, depth and structure of the soil, and microrelief were taken into account. Meteorological data of the Pozhyzhevska avalanche station of the Ministry of Emergencies of Ukraine were taken into consideration.

Studies on the effects of cattle and sheep grazing were conducted in areas with different numbers of animals per hectare: low (≤0.5), moderate (0.6–1.4), or intensive (≥1.5). The impact of raw material harvest (aboveground or underground parts) on medicinal and ornamental plants was assessed. Data collection was conducted both on permanent research plots and using single or multiple irregular route studies (Dylis, 1974; Pfadenhauer et al., 1986; Zlobin, 1989; Gibson, 2002). Permanent research plot methods provided multiple accounting of the same parameters on constant transects. They lasted from several to 40 years and were performed using visual assessments or precision instruments. The distribution patterns of individuals within populations were mapped on transects on a scale from 1:100 to 1:1. The number and density of the population and the age and vitality of individuals were taken into account. The long-term observations of the parameters of mapped individuals made it possible to study the ontogenesis of plants, as well as the dynamics of vitality and reproduction in populations and their response to anthropogenic and natural impacts. Mapping was performed on transects with an area of 20–25 m^2 in meadow and shrub coenoses with the size of the accounting squares being 0.50×0.50 m (Dylis, 1974) and, if necessary, on smaller plots of 0.20×0.20 m also.

Traditional methods were used to study the ontogeny and age structure of populations, their numbers, density, reproduction, and viability (Kyyak, 2013). Age status of the individual plants – seedling (p), juvenile (j), immature (im), virginile (v), generative (young – g_1, middle aged – g_2, obsolescent – g_3), subsenile (ss), and senile (s) – was determined for each targeted species, taking into account their life form. Each age status corresponds to a certain stage of ontogeny with a set of particular individual qualitative and quantitative traits. In general, plant ontogeny involves stages of growth, achievement of reproductive functions, aging, and dying (Ulanova, 2000; Gatsuk et al., 1980). The ontogeny of target species has been studied for 5–30 years under different environmental conditions. At the beginning of the study of target species, 25 individuals of each age were marked with colored durable marks near the place of their rooting for clear identification. In the following years, seedlings or shoots that appeared within the experimental plots were additionally marked. Any changes that had occurred in the morphological structure of marked plants, their basic quantitative and qualitative parameters, or their death were recorded annually. Thus, ontogenesis was studied by observing the development of individuals from seed to aging and death. The duration of individual age states was determined mainly by direct observations of marked plants (Kyyak, 2013).

The age composition of populations is determined on the basis of the ratio of the individuals in different age groups. The number and density of populations were calculated on transects and additional accounting sites, located representatively in different spatial components of the population, from its core to the periphery (Rabotnov, 1969). Population density was determined by the number of individuals per 1 m^2. The viability of individuals and populations was assessed as high, medium, or low (Yermakova, 1976; Gatsuk et al., 1980; Zlobin, 1989, 2009; Malynovsky, Tsaryk, 1991).

Results

Carex curvula showed significant negative changes in its demographic structure. The adverse changes affected primarily the peripheral part of the population at its lower altitude boundary (Table 1). This isolated coenopopulation occupies about 1000 m^2 habitat at the lowest part (1840–1860 m a.s.l.) of the species range in the Ukrainian Carpathians at a distance of about 4 km from the core area of the populations of *C. curvula*. In winter, this area is characterized by heavy winds and shallow snow cover (up to 0.5 m). Vegetation cover ranges within 85–100%. The habitat is intersected by a tourist trail with moderate attendance. Less than 10% of *C. curvula* is subject to trampling. Due to high resistance, trampling does not have a significant impact on the demographic structure and general dynamics of the *C. curvula* coenopopulation. Other

Table 1. Changes in the number of age groups of the *Carex curvula* population on Mt. Drabyny during 1999–2018 (Chornohora massif, Ukrainian Carpathians).

Year	Population loci, no.	Total number of individuals (%)	Number of age groups, individuals (%)						
			j + im	v	g_1	g_2	g_3	ss	s
1999	1	780	45	530	76	8	-	115	6
	2	75	5	16	21	9	19	4	1
	3	41	4	23	10	2	2	–	–
	Total	896 (100)	54 (6)	569 (64)	107 (12)	19 (2)	21 (2)	119 (13)	7 (1)
2018	1	190	112	39	–	–	–	37	2
	2	43	15	13	3	–	2	10	–
	3	36	11	16	1	–	1	7	–
	Total	269 (100)	138 (51)	68 (25)	4 (2)	–	3 (1)	54 (20)	2 (1)

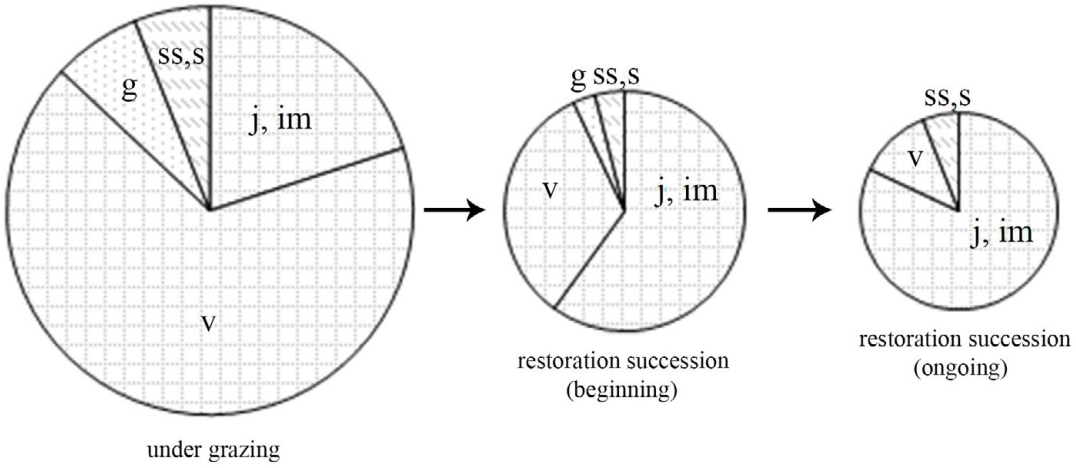


Fig. 1. *Saussurea alpina* age structure changes as a result of restoration succession (Mt. Komyn, Svydovets Ridge). Under grazing – moderate grazing; restoration succession (beginning) – grazing cessation, restoration succession, green alder shrub pervasion; restoration succession (ongoing) – green alder patches extension, increasing shrub canopy thickness.
Note: Here and in the following figures, area of the circle corresponds to the population size; j, im, v, g_{1-3}, ss, s – age status of the individuals.

current human impacts are absent. The restoration processes that began after the cessation of grazing in 1986 are rather slow and insignificant. Consequently, warming air and soil temperature, and a decrease in soil moisture, is a decisive factor in the negative dynamics of the *C. curvula* population.

The most dramatic negative changes have occurred in the last 10 years. Significant changes have occurred in the juvenile and generative parts of the age spectrum. The share of generative individuals in the coenopopulation has decreased from 16% to 3%. All indicators of vitality (height of shoots, turf size, number of generative shoots, seed productivity) of generative plants have decreased in all loci. Also, the proportion of virginile plants has decreased from 64 to 25%. At the same time, the decrease in the population as a whole from 896 to 269 individuals has been accompanied by a significant increase in the number of juvenile plants, both in absolute numbers (from 54 to 138 individuals) and in percentage (from 6 to 51%).

The consequence of climatogenous changes is also a significant decline of *C. curvula* vitality. Primarily, this concerns the reproductive individuals. If at the beginning of observations (in 1999), the height of generative plants reached an average of 36 cm, in recent years, it has been only 15–20 cm. The number of generative shoots on a generative middle aged individual has decreased from eight to two or three over these years.

Since 2016, generative middle-aged plants are completely absent in the population. In recent years, young and old generative individuals have formed no more than one generative shoot. The diameter of turfs of the virginile plants has decreased from 2–3 (4) cm to 1 cm. All these demonstrate the gradual degradation of this population, which is accompanied by temporary false rejuvenation.

The reason for the negative demographic changes of *Saussurea alpina* is natural succession. On the rocky steep slope of Mt. Komyn (northern exposure at an altitude of 1650 m a.s.l., Svydovets Ridge), *Alnus viridis* (Chaix.) D.C. expands and displaces *Saussurea alpina* during natural restoration succession in response to grazing cessation. Green alder canopy development leads to a drastic reduction in the numbers, density, and loss of vitality of *S. alpina*. Its age structure acquires signs of pseudo-rejuvenation (Fig. 1).

It was found that *Gentiana acaulis* is very sensitive to shading. Depending on their age, vitality, as well as the degree and mode of shading, adult plants of *G. acaulis* die off gradually within 1–4 (6) years. This process begins with termination of flowering and fruiting and simultaneous increase in the vegetative mobility of the ramets (rate of vegetative mobility increases from 2 to 9 cm per year compared to slight shading). Then, shoots and leaves become thinner and elongated, metamers are lengthened, maternal individuals disintegrate into separate fragments, and vegetative mobility of ramets reduces up to 4–6 cm/year. Finally, false rejuvenation of the ramets (acquisition of immaturity or juvenile attributes) occurs simultaneously with further reduction of the number and vitality and at the very end, their extinction occurs. At the beginning of degradation, if shading decreases, it is quite possible for individuals to reverse to a generative state as well as to regain their viability. However, in both cases, over a period of time, the age structure has the features of a young population, although in reality, it is under threat. Consequently, because of the decline in number, we tend to recognize it as false or pseudo-rejuvenation, but not rejuvenation of the *G. acaulis* population.

The graph presented in Fig. 2 displays false rejuvenation of the population of *Heracleum carpaticum.* Due to its vulnerability to grazing, on mountain pastures, targeted removal or damage by cattle has led to simultaneous decrease in the number of adult plants as well as the size of the whole *H. carpaticum* population and increase in the proportion of young individuals. Instead, in remote places, on the rocky slopes with very limited grazing, age structure of its population remains balanced.

The reason of the false rejuvenation may be the intensive picking of ornamental plants. As a result of the systematic removal of the most attractive generative plants from populations, middle-aged and old generative individuals are disappearing. Young generative group is occasionally replenished from the virginal individuals. However, they do not reach the middle-aged state due to harvesting. As a result, the number and density of populations

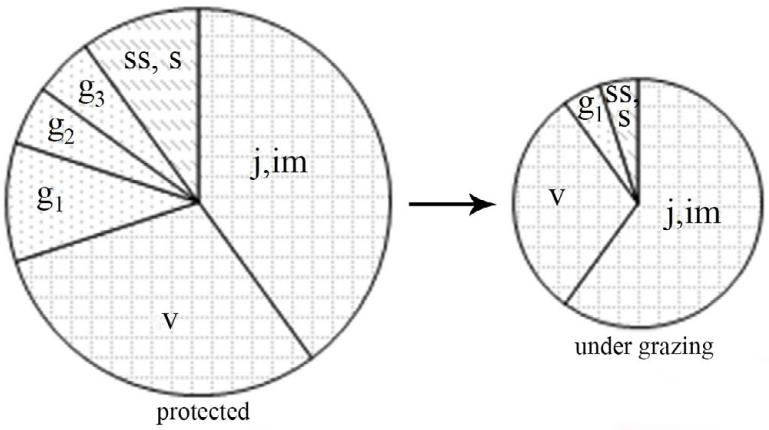


Fig. 2. Effect of grazing on the size and age structure of the populations of *Heracleum carpaticum* on Mt. Chivchyn.

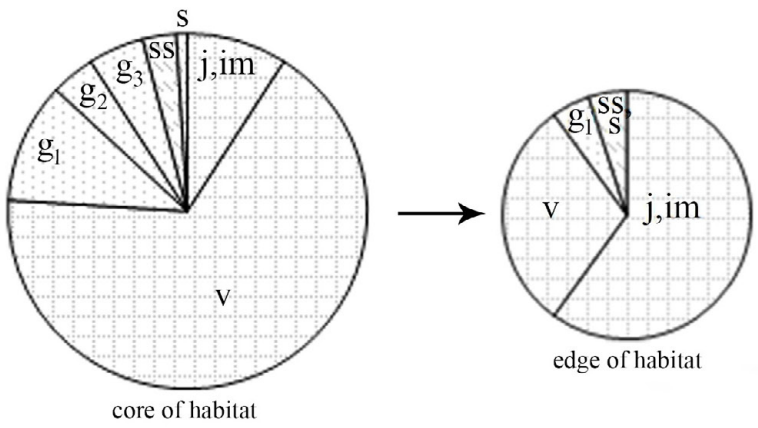


Fig. 3. *Leontopodium alpinum* age structure changes due to picking flowers (Mt. Dragobrat, Svidovets Ridge).
Note: Core of habitat – inaccessible rocks, without disturbance; edge of habitat – reachable places, with regular damage.

decrease. Their age structure is dominated by seedlings, juvenile, and virginal plants. In particular, such structure is typical for populations whose core part is located on inaccessible rocks while the periphery is accessible and intensively visited. In the core part, age composition of the population is full-fledged, with a high percentage of generative plants and higher density. On the periphery, the population density is less, middle-aged and old generative plants are absent, while pregenerative individuals predominate (Fig. 3).

Similar results were obtained during experimental removing (once per summer season) of aboveground phytomass of *Ranunculus thora.* It has led to a sharp decline in the number of generative plants and false rejuvenation of the whole population.

An extreme wind and temperature regime on the Chornohora Ridge is the main reason for the decrease in the viability of individuals and populations of *R. thora*. As a result, two separate populations of *R. thora* on Mt. Spytsi (1750–1850 m a.s.l., E slope) and on Mt. Berbeneska (1980 m a.s.l., NW slope), where the average daily air temperature during the growing season is lower by 2–2.5 °C, have a different age structure.

On the steep rocky slopes and crevices of rocks on Mt. Berbeneska with almost complete absence of soil as well as extremely low temperatures and intense winds, the duration of ontogenesis is prolonged (particularly in the pregenerative stages) and the generative middle-aged state may not be reached. As a result, the age structure of the population acquires signs of false rejuvenation (Fig. 4).

Thus, a generalized pattern of population degradation during deterioration of living conditions consists of two phases (Fig. 5). Initially, as a result of moderate deterioration of the environmental conditions, the total population size decreases due to decline in the number of generative and virginal individuals. High vitality individuals, in particular, g_2, are not formed (Fig. 5, unfavorable). With further critical deterioration of living conditions, generative individuals are not formed at all (Fig. 5, critical). The number of virginal individuals continues to decline. In both phases, with the background of decrease in total population size, the percentage of young individuals in the population increases.

Discussion

The probable causes of pseudo-rejuvenation of populations can be various natural and anthropogenic factors. Frequent and regular

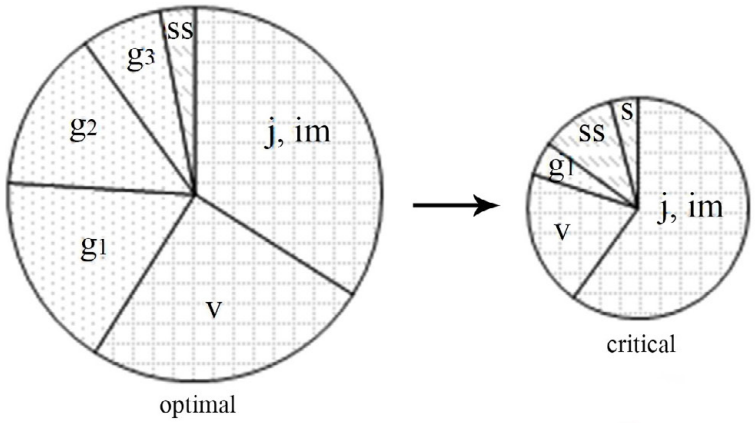


Fig. 4. The effect of pseudo-rejuvenation in populations of *Ranunculus thora* due to environmental deterioration.
Note: Optimal – favourable soil, coenotic and microclimatic parameters; critical – extreme temperature and wind conditions, soil erosion.

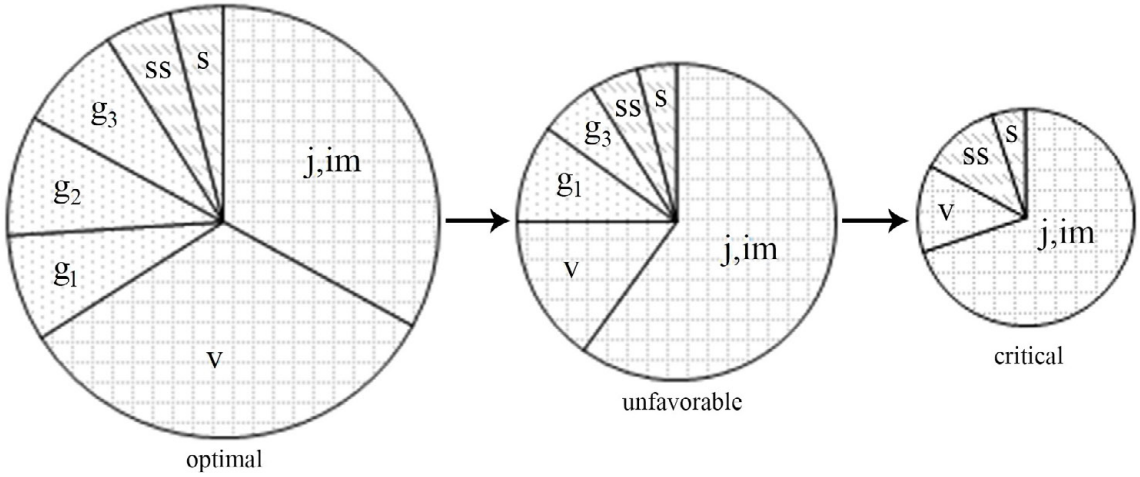


Fig. 5. Generalized scheme of pseudo-rejuvenation and plant populations' demographic structure due to deterioration of the environmental conditions.

plucking of whole plants or their parts during the harvesting of medicinal and decorative species is a major threat to *Leontopodium alpinum* as well as *Rhodiola rosea* L., *Ranunculus thora, Gentiana lutea* L., and *G. punctata* L. in the Ukrainian Carpathians. In most mountainous regions in Ukraine, these species are represented by small populations with a damaged spatial structure and have reduced viability and age composition with evident pseudo-rejuvenation. The percentage of individuals in the generative and post-generative groups decreases or completely disappears. At the same time, the proportion of young pre-reproductive plants increases. Due to reduction of seed yield, the population size decreases. The remnants of these populations or their single fragments remain only in remote inaccessible localities, that is, on rocks, steep slopes, and so on.

The vulnerability of plants to the removal of aboveground phytomass depends on their age and the frequency of removal. Some species are sensitive to the removal of flowering shoots only at a young age (g_1), when their leaves form a significant proportion of the assimilating surface of the whole individual. Young generative individuals are especially vulnerable in the first years of flowering. The next year, after the removal of generative shoots, plants usually do not flower and pseudo-rejuvenation of population occurs. Such a reaction to mechanical damage is typical for the polycentric species, which form clones with multiple shoots (*Gentiana acaulis, Doronicum clusii* (All.) Tausch, *Ptarmica tenuifolia* (Schur) Schur).

The effect of pseudo-rejuvenation could be the result of selective consumption of adult and virgin plants by livestock during grazing. Seedlings and young plants suffer less. Under the influence of grazing, some species can demonstrate rejuvenation of populations due to stimulation of their vegetative reproduction. This is a peculiar feature of many species of grasses and sedges.

However, in some species, grazing does not stimulate vegetative reproduction. Such species are especially vulnerable to graz-

ing even with low intensity and often have a structure with signs of pseudo-rejuvenation. In areas with intensive grazing, their populations degrade and fall out of the phytocenoses.

The climate change that has taken place so far causes the disappearance of optimal conditions needed for the development of generative individuals of *Carex curvula*. As a result, middle-aged generative plants have completely disappeared from the population and the numbers of young and old generative individuals have significantly decreased. These age groups are formed in the narrowest range of the most optimal living conditions. During the study period, a significant number of generative individuals refilled the subsenile group, but most of them died. Instead, relative participation of pregenerative plants that are able to exist in poorer conditions has increased in the population. It is argued that, in case of deterioration of living conditions, the formation of a "pseudo-juvenile" population structure with a predominance of young individuals and a small proportion of generative individuals is typical for plants of different life forms.

In recent decades, ecological restorative successions form a significant natural threat to many rare species. Their consequence is the rapid spread of trees and shrubs on high mountain meadows, and increased shading, which is a threat to low-competitive species. Transformation in coenotic conditions leads to change in the duration of ontogenesis and individual stages of plants, and acquirement of the signs of pseudo-rejuvenation by population.

Conclusion

It is important to distinguish between the concepts of "rejuvenation" and "pseudo-rejuvenation" of the population. Rejuvenation is the process of increasing the proportion of young individuals in the structure of a population, provided its total number and vitality are maintained or increased. Pseudo-rejuvenation means the process of increasing the percentage of young individuals in a population, but with a simultaneous decrease in its total number and/or vitality.

The fundamental and indispensable sign of rejuvenation of the population is a positive dynamic. In contrast, pseudo-rejuvenation is an indicator of negative exogenous or endogenous changes and is inherent in degrading populations or populations in adverse living conditions. False rejuvenation can be caused by both natural and anthropogenic factors.

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