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URAL ENDEMIC SPECIES OF THE GENUS *Minuartia* L.: ONTOGENY, POPULATION STRUCTURE, AND DYNAMICS*

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The authors studied two endemic species of minuartia that occur intermittently and form small, isolated populations. Characteristics of these species' biomorph and stages of ontogeny are given; on the basis of long-term observations, changes in the age structure of populations are traced.

Preservation of the Earth's biological diversity is one of the most important problems of modern biology. Steps can be taken to protect rare and endangered plants only on the basis of knowledge of their extent, ecological peculiarities, life strategy, and reaction to natural and anthropogenic factors. Endemic plants are frequently among the most vulnerable elements of regional floras. In the flora of the Urals, endemics are represented, for the most part, by species with a small range and intermittent occurrence that exist in the form of small, isolated populations. Study of small, isolated plant populations and clarification of the mechanisms of their existence in conditions of growing anthropogenic actions are of theoretical, as well as practical interest (Gorchakovskii and Zueva, 1984, 1993; Zarzycki, 1976).

The objects of the present investigation were two species of minuartia endemic to the Urals: Krasheninnikov's minuartia (*M. kraschenіnnikovii* Schischk.) and Helm's minuartia (*M. helmii* (Fisch. ex Ser.) Schischk.). Both species belong to the group of rocky mountain-steppe endemics (Gorchakovskii, 1969), occur intermittently, and are represented by small, isolated populations separated from each other by edaphic and cenotic barriers. Krasheninnikov's minuartia is an endemic of the Southern and Central Urals and grows in mountainous rocky steppes and on limestone outcrops along the banks of rivers. Helm's minuartia is an endemic of the Southern, Central, and, partly, Northern Urals and grows in mountainous and foothill rocky steppes, on rock (primarily limestone) outcrops along the banks of rivers, and also on outcrops of dunite, gabbro, and pyroxenite at the summits of some low mountains. In comparison with the previous one, this species has a more extensive range and wider ecological amplitude; however, it also occurs intermittently and is closely connected with a rocky outcrop substrate.

Field investigations were conducted from 1979 through 1993 in the Central and, partly, Northern Urals in characteristic growing places for both species of minuartia. In the first stage of the work, we clarified peculiarities of these plants' ontogeny. It proved possible to distinguish the following categories of individuals according to their age condition: plantlets (pl), juvenile (j), immature (im), young (g_1), middle-aged (g_2), and old generative (g_3), subsenile (ss), and senile (s). To clarify the age structure and population dynamics, we laid out permanent sample areas 100 m^2 in size. Each sample area was broken up into 1 m^2 squares, on which we recorded all minuartia individuals for a number of years, with their distribution by age conditions. In analyzing the populations' age spectra, subsenile individuals were combined with senile ones. Each individual was marked, which made it possible to trace the appearance of plants, their transition from one age condition to another, and death. On the basis of these observations, we were able to reveal year-by-year changes in the density and age structure of populations of endemic species of minuartia. To characterize population density, we used the density index (number of individuals of a given species per 1 m^2). The populations were given names according to their geographic locations.

Both species of minuartia are tap-rooted dwarf semishrubs that form a multiheaded stem-root (caudex). The lower parts of the shoots are perennial, slightly lignifying; the upper parts are herbaceous and die back for the winter. The bush sometimes

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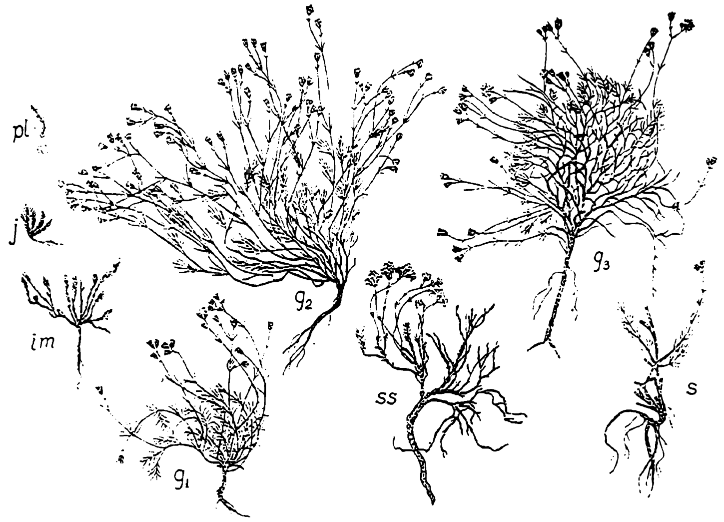

Fig. 1. Age conditions of Krasheninnikov's minuartia: pl) plantlet, j) juvenile, im) immature, g_1) young generative, g_2) middle-aged generative, g_3) old generative, ss) subsenile, s) senile.

acquires the form of a loose pillow (this is especially characteristic of Helm's minuartia growing in high mountains). The regeneration buds on overwintering parts of the stems are frequently covered by mosses, lichens, and sometimes a layer of fine earth.

Krasheninnikov's Minuartia. In the life cycle of this species (Fig. 1), formation of individuals begins from a plantlet that has a thin rootlet and a short subcotyledon node (hypocotyl) crowned with two lanceolate cotyledons. Then, from the apical bud a supracotyledon shoot appears, bearing small, setiform leaflets, and the cotyledons die back. The main (axial) shoot grows monopodially for several years, and buds are set in the axils of the leaves.

The transition to a juvenile state usually coincides with dieback of the tip of the main shoot and formation of several lateral shoots from axillary buds: second-order axes. Further formation of the bush occurs by means of sympodial branching: the tips of second-order axes die back; third-order axes form from axillary buds; their tips, in turn, die back, and fourth-order shoots arise, etc. Juvenile individuals are little plants with shoots that are still thin and slightly branched.

Immature individuals have a thick, long root, a formed caudex, and longer and more branched shoots forming the skeletal foundation of the future bush.

On young generative individuals one can already discover all of the features of a dwarf semishrub's life form: a fairly well developed root going down into cracks in the rocks, a formed caudex, skeletal branches in a bushy arrangement, the lower (basal), lignified parts of which overwinter, remaining viable, while the upper, herbaceous parts die back in the fall, with young shoots forming from axillary buds on the basal parts in the spring of the following year. Formation of shoots from dormant buds in the lower, more lignified part of basal shoots also helps to increase the bush's density. There are still relatively few generative shoots; they end in solitary flowers or inflorescences of the dichasium type consisting of 2-3 flowers.

The bush of middle-aged generative individuals reaches the greatest development (height 8-12 cm, width 12-22 cm); it is fairly dense and very branched, with numerous generative shoots bearing 2-3 inflorescences. The leaf apparatus is well developed, and there are many vegetative shoots. The weight of the herbaceous parts of the shoots that die back every year exceeds the weight of the overwintering, lignified, basal parts of the shoots. The caudex is fully formed, and the root is fairly well developed, going down deep into the soil, and branched.

Old generative individuals still preserve the viable skeletal foundation of the bush, but the weight of annual herbaceous parts is already less than the weight of perennial, lignified parts of the shoots. There are many shoots that have died back, belonging to higher-order axes (third, fourth, etc.). Generative shoots are not as numerous, and some of them have a single flower.

Subsenile individuals are characterized by dieback of the greater part of the skeletal branches; usually only one skeletal branch remains alive, bearing a few foliated shoots with shortened internodes, and even fewer generative shoots.

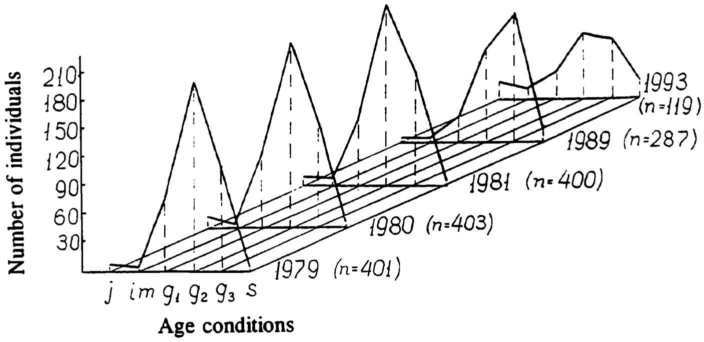

Fig. 2. Dynamics of age structure and density the "Kur'i" population of Krasheninnikov's minuartia (n — total number of individuals on 100 m^2).

On senile individuals, almost all of the skeletal branches have not only died back, but have decomposed and fallen off. On the remaining basal parts of one or two skeletal branches there are a few vegetative shoots, usually with shortened internodes. Sometimes, a generative shoot with 1-2 flowers appears (but the seed buds are underdeveloped, and seeds never form).

We studied two populations of Krasheninnikov's minuartia: the "Kur'i" population on the Pyshma River, and the "Smolinsk" population on the Iset River.

The Kur'i population is located on the steep slope of a limestone cliff facing the Pyshma River, near the "Kur'i" resort. A vertical scarp prevents fine earth from getting onto the slope from above. There is a small amount of fine earth only in cracks between the blocks, where Krasheninnikov's minuartia grows. The surface of the cliff is bare; there are no other species of vascular plants and no competition between species. This population characterizes one of the first stages of colonization of an outcrop substrate by vascular plants.

The Smolinsk population was formed on a limestone outcrop at the Iset River near the Smolinsk caves in the vicinity of the "Metallurg" resort lodge not far from Kamensk-Uralskii. The outcrop has been subjected to long and intensive weathering; fine earth has accumulated not only in cracks, but also on the surface of the blocks in places. Besides the predominant species (Krasheninnikov's minuartia), *Dianthus acicularis, Elytrigia pruinifera, Veronica spicata, Artemisia sericea, Galium verum, Thalictrum foetidum*, etc. are found here. This is a more advanced stage of formation of vegetation on an outcrop limestone substrate; however, individuals and clumps of Krasheninnikov's minuartia occupy a strictly defined position in the cracks of limestone blocks; competition with other species is slightly expressed.

During the period from 1979 through 1981, the Kur'i population (Fig. 2) had fairly high density (index 4.01-4.03). It was a normal, full-membered population, and all age groups were represented in its composition. However, generative individuals were clearly predominant; and among them, middle-aged ones. There were very few juvenile and immature individuals, which is apparently explained by the fact that almost all of the places accessible to the plants were occupied by generative individuals. There were almost no senile individuals. In 1989, the population had acquired features of an aging one: its density had dropped to 2.87; old generative individuals were now predominant; and the portion of senile individuals had risen sharply. In 1993, the declining wave in the population's dynamics had almost ended: the density had dropped to 2.16; the older generation had died back; and many individuals had moved to a senile state. However, a lot of juvenile and immature individuals had appeared, which marked the onset of an ascending wave in the population's dynamics.

In 1979-1981, the Smolinsk population was also a normal, full-membered one, but somewhat less dense (index 3.21-3.39). Generative individuals were predominant in it; and among them, middle-aged generative individuals especially, although during these years a trend was revealed toward an increase in the portion of old generative individuals. In the first years there were fairly many immature individuals. In 1982, old generative individuals began to predominate, although the population density still remained at approximately the former level (3.26). In 1993, a sharp reduction in the number of generative individuals was observed, with an increase in the number of senile individuals. The density decreased by 1.19. A lot of juvenile individuals appeared. Apparently, this reflects one of the stages of replacement of the old generation of plants by a younger one. The relatively low density of the Smolinsk population (in comparison with the Kur'i population) is explained by the greater weathering of the rocky substrate and the larger amount of fine earth accumulating not only in cracks, but also on the surface of the rock blocks, which favors invasion of competing species of vascular plants.

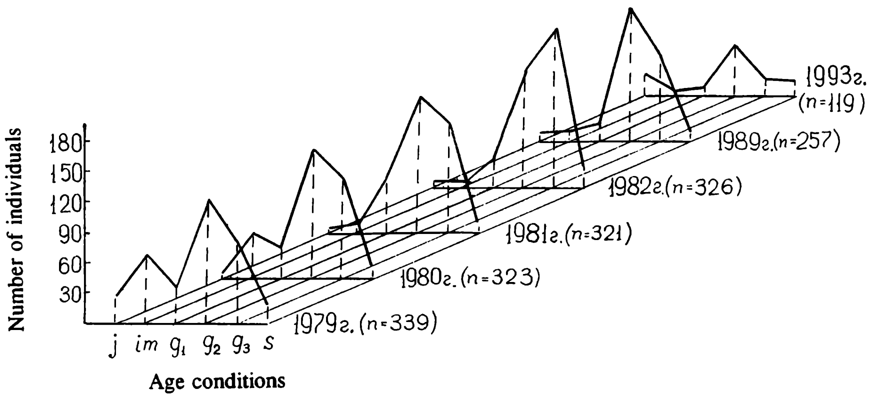

Fig. 3. Dynamics of age structure and density of the "Smolinsk" population of Krasheninnikov's minuartia.

Helm's Minuartia. The phases of this species' ontogeny are shown in Fig. 4. The plantlet has a thin rootlet, short hypocotyl, two lanceolate cotyledons, and a supracotyledon node covered with narrow lanceolate leaflets, in the axils of which buds are set. The main axial shoot grows monopodially for several years.

In juvenile plants, the tip of the axial shoot dies back; second-order shoots form from axillary buds; and after their tips die back, third-order shoots, as well. The root is longer.

Immature individuals already have the whole skeletal foundation of the future bush; the shoots are densely foliated; and the root is branched.

Young generative individuals have a root that goes deep down into cracks, is branched, and expanded in the upper part. The caudex is clearly expressed. The lower skeletal branches are raised up and bear vegetative and generative, single-flowered shoots.

In middle-aged generative individuals of the plants, the bush is fully formed, reaches its greatest size (height 6-15 cm, width 7-24 cm), and is fairly dense, on account of multiply branched axial shoots. The leaf apparatus is well developed, and vegetative shoots have lengthened internodes. Generative shoots are numerous, most of them with 2-3 flowers in an inflorescence of the dichasium type. Some generative shoots are single-flowered. The root is very branched and goes down deep into cracks.

Old generative individuals have a looser bush (as a result of dieback of part of the skeletal branches). The root and base of the skeletal branches are thicker. Foliation is not as dense, and vegetative shoots are shortened on account of a reduction in the length of internodes. There are fewer generative shoots, and they are all single-flowered.

Subsenile individuals usually keep only 1-2 skeletal branches; the rest die back. On the caudex, remains of dead branches not completely separated from the plant can be seen. Vegetative shoots are shortened. There are no generative shoots, or only one single-flowered one.

In senile individuals, all of the skeletal branches have died back completely or almost completely, and the greater part of them has separated from the plant. Only the basal parts of 1-2 skeletal branches remain viable, from which a few shortened vegetative shoots branch out from dormant buds. There are no generative shoots.

Study of populations of Helm's minuartia was done in two places: on Kolpak Mountain and at Tal'kov Kamen.

The "Kolpak Mountain" population is located on the rocky summit of one of the relatively low mountains of the Central Urals: on Kolpak Mountain (956 m above sea level), which belongs to the group of Kytlym Mountains that also includes Konzhakovskii and Kos'vinskii Kamni. The mountain's summit is composed of olivine gabbro. Large blocks of rock only provide refuge for lichens. Helm's minuartia grows in accumulations of fine earth between rock blocks. There, *Empetrum hermaphroditum* and *Thymus paucifolius* are occasionally found.

The "Tal'kov Kamen" population is connected with the deep quarry of the same name near the Sysert settlement in Sverdlovsk Oblast, where there was formerly a mine that produced talc. The bottom of the quarry filled up with groundwater, and a deep lake formed there. On the very steep, in places vertical, scarps of the quarry, which are composed of talc and face the lake, Helm's minuartia grows in abundance. There are no other species of vascular plants there and no competition between species.

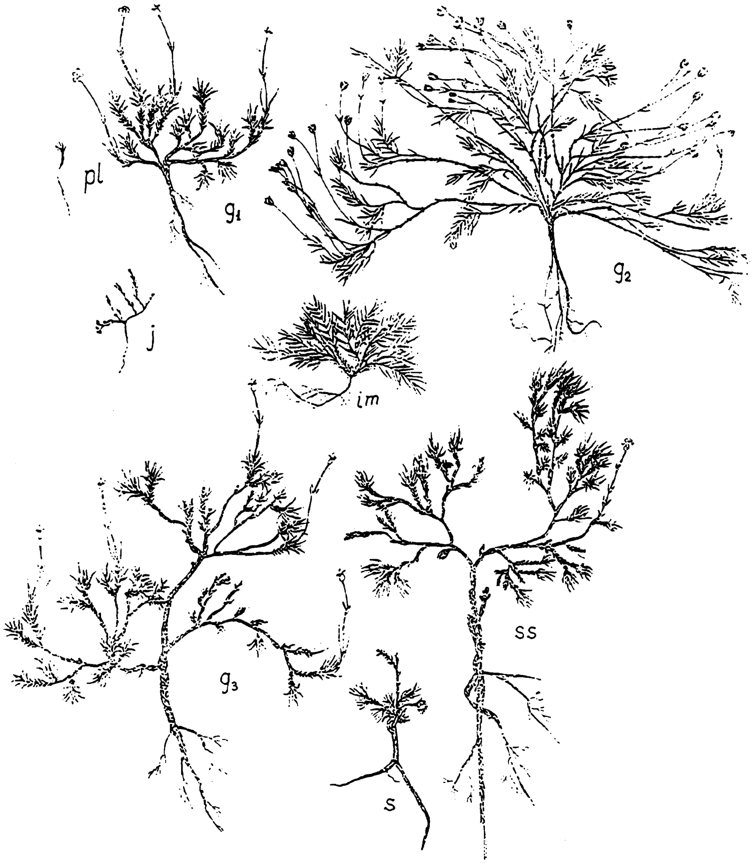

Fig. 4. Age conditions of Helm's minuartia. Notations are the same as in Fig. 1.

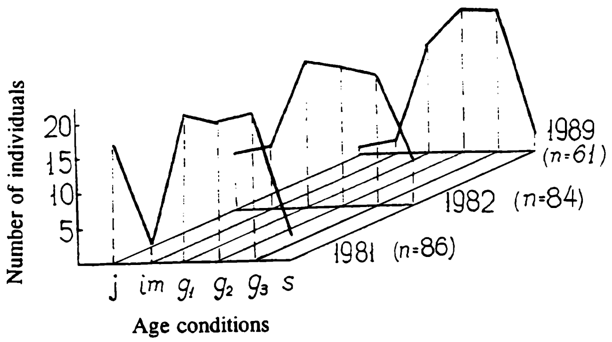

Fig. 5. Dynamics of age structure and density of the "Kolpak Mountain" population of Helm's minuartia.

The Kolpak Mountain population of Helm's minuartia (Fig. 5) is characterized by low density (0.61-0.86), which is explained by peculiarities of the substrate. This plant can grow there only in cracks where fine earth accumulates, while the greater part of the surface is represented by large rock blocks. In 1981, the population was a normal, full-membered one, with a predominance of generative individuals and a fairly large number of juvenile ones. The density index was 0.86. In the next year, 1982, the ratio between juvenile and immature individuals evened out, while on the whole the nature of the age spectrum stayed the same. In 1989, signs of the population's aging became noticeable, which was reflected in a shift of the age spectrum in the direction of old generative individuals, with a reduction in population density (0.61).

A distinctive feature of the Tal'kov Kamen population (Fig. 6) is its very high density (from 10.52 to 12.33). This is connected with the fact that the surface of the weathering talc is dissected by numerous cracks, in which the products of its weathering accumulate. These are precisely the places that serve as niches where colonization by Helm's minuartia is possible.

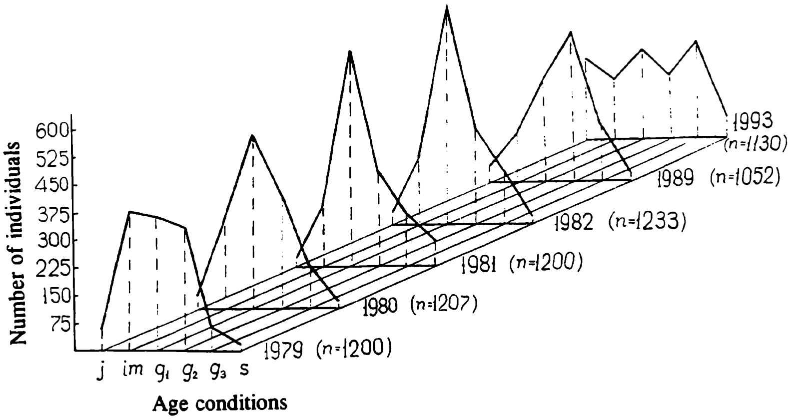

Fig. 6. Dynamics of age structure and density of the "Tal'kov Kamen" population of Helm's minuartia.

In 1979, the population was a normal, full-membered one, and generative individuals were predominant in the age spectrum, with a preponderance of young generative individuals. In subsequent years (1980, 1981, 1982), the age spectrum kept its former features on the whole, but a clear predominance of middle-aged generative individuals was revealed. In 1989, there was a slight reduction in density (10.52), while the former ratio of age groups was preserved in general. The spectrum in 1993 reflects the superposition of two waves: a declining one (predominance of old generative individuals, a large number of senile ones), and an ascending one (introduction of a new generation, reinforcement of the position of juvenile individuals). In that year, the population density rose somewhat (11.30).

CONCLUSIONS

Krasheninnikov's minuartia and Helm's minuartia belong to the same life form (tap-rooted dwarf semishrubs that form a caudex), are included in the same group of rocky mountain-steppe endemics, and are largely similar in their ecology. But detailed analysis reveals certain differences between them that are worthy of attention. Existing in the form of small, isolated populations, they rarely grow together; usually each species occupies its own ecological niche. The extent of both species is bounded by the limits of the Ural mountain region. However, Helm's minuartia has a somewhat larger range and wider ecological amplitude, extending to the Northern Urals, where it is found not only on limestone outcrops along the banks of rivers, but also in high mountains on outcrops of dunite and gabbro. Both species grow in places where competition on the part of other vascular plants is slightly expressed or completely absent. This property is manifested most clearly for Helm's minuartia, which frequently colonizes places inaccessible to other plants, for example, vertical limestone outcrops along the banks of the Vizhai and Northern Toshemka Rivers, large-block detritus on mountaintops, or the very steep slopes of a talc quarry.

In their life strategies, both Krasheninnikov's minuartia and Helm's minuartia are classified, in L. G. Ramenskii's terminology (1971) as explerents or, in J. Grime's terminology (1979), as ruderals. They rapidly colonize an outcrop rocky substrate, being satisfied with a small amount of fine earth and humus accumulating in cracks in the rocks. Their populations occupy certain sections of the rocky surface until continuous renewal of the surface occurs there as a result of weathering and erosion. In the course of this process, ever newer and newer sections of bare rock surface appear, with a small amount of fine earth in the cracks. When the surface is covered with a layer of fine earth and exposure of the rocky substrate ceases, the endemic minuartias are crowded out by other plant species.

However, these plants have certain inherent features of patients (according to Ramenskii) or stress-tolerants (according to Grime), since they grow on rocks devoid of a formed soil cover, are not always sufficiently sheltered by snow in the wintertime, and in the summer they are forced to withstand sharp temperature fluctuations (the rock surface is strongly heated during the day and cools off at night), temporary moisture deficiency, the desiccating action of wind, etc.

The population density of endemic minuartias depends on the composition of the rock, physical properties of the weathering crust, the nature and degree of weathering, and also on the presence of competing species of vascular plants. The greatest differences in density of individual populations are noted for Helm's minuartia: the lowest in the high-mountain population and the highest in the population on a talc outcrop.

Populations of the studied species are subject to wave changes in age structure and density, which is due to the regular transition of individuals from one age condition to another, as well as the meteorological conditions of individual years. There is a succession of ascending waves (mass appearance of juvenile and immature individuals) and declining ones (destruction of the generation of generative individuals). When a generation of generative individuals has already formed, it occupies almost all of the places accessible to the plants; therefore, the possibilities of appearance of young individuals are very limited. At that time comes a period of relative stabilization of the population's age structure, which lasts for several years.

We cannot fail to notice a certain synchronism in the onset of the period of destruction of the generation of generative individuals and mass dieback of senile individuals in different populations of the same species remote from each other. Apparently, this is due to stressful meteorological situations created in the course of the growing season in individual years (prolonged absence of precipitation, heat wave, etc.).

The small, isolated populations of Ural endemic species of minuartia are inseparably connected with a rocky substrate. The places where they grow are frequently subjected to various anthropogenic actions (recreation, grazing of livestock, gathering of rocks for construction and other purposes), which creates a threat of extinction for these rare plants. In order to protect endemic minuartias it is necessary to create reservations where removal of the territory from economic use would be combined with measures to assist regeneration of these species (removal of sod, elimination of competing plants).

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