ISSN 0096-7807

Vol. 15, No. 3, May-June, 1984

January, 1985

SJECAH 15(3) 103-160 (1984)

THE SOVIET JOURNAL OF ECOLOGY

ЭКОЛОГИЯ/ÉKOLOGIYA

TRANSLATED FROM RUSSIAN

CONSULTANTS BUREAU, NEW YORK

AGE STRUCTURE AND DYNAMICS OF SMALL ISOLATED POPULATIONS OF URAL ENDEMIC MILK VETCHES

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UDC 581.522;582.736;581.526.4

Four endemic rocky alpine steppe milk vetch species were studied; the morphological features of their age states were clarified; structural changes in the populations were traced against the background of anthropogenic influences.

The Ural, rocky alpine steppe endemic group in the Urals and Cisural Area (Gorchakovskii, 1969) is sharply isolated both geographically and ecologically. The plants belonging to it are distributed primarily in the southern part of the Ural mountain region, where they grow in rocky alpine steppes and on crags. Furthermore, endemics of this group are found outside the main distribution range to the north in a number of isolated habitats on exposures of various rocks, primarily carbonates (limestone, gypsum).

The narrow specialization of rocky alpine steppe endemics for existence under strictly defined environmental conditions on a rocky substrate with moderate competition from other plants results in a patchy distribution even within the main distribution range. This patchiness has been further intensified recently due to increasing anthropogenic influences (plowing, livestock grazing, recreation). These endemics are the most vulnerable part of the local flora; a change or destruction of biotopes results in their extinction, and the ecological niches that are freed are filled by synanthropic plants with a broad ecological amplitude and an extensive distribution range (Gorchakovskii, 1979; Gorchakovskii and Shurova, 1982).

Study of rocky alpine steppe endemics is of interest from a theoretical point of view to elucidate the patterns of existence of plant species in the form of small isolated populations. The problem of small plant populations has recently gained much importance and is of interest to botanists and ecologists (Zarzycki, 1976). Studies of such type are important in connection with the fact that the fractionation of plant populations and the reduction of their numbers under human influence is a characteristic feature of the modern epoch. In the near future the extensive and abundant populations of many species will pass to the category of small populations. On the other hand, the study of small endemic-plant populations is also necessary in practical terms for the organization of their monitoring and the development of conservation measures.

This paper presents the results of a study of the age states, age structure, and response to anthropogenic influences of small isolated populations of characteristic representatives of the group of rocky alpine steppe endemics in the Urals and Cisural Area, the endemic milk vetch (*Astragalus*) species. With respect to volume, the populations studied were in most instances larger than cenopopulations in the understanding of T. A. Rabotnov (1975) and A. A. Uranov (1975).

The populations of four milk vetch species were studied: *A. karelinianus* M. Pop., *A. helmii* Fisch., *A. clerceanus* Iljin et Krasch., and *A. kungurensis* Boriss. The intrapopulation and interpopulation variability of these species was characterized in an earlier-published work (Gorchakovskii and Zueva, 1982).

Studies were conducted at the following sites: For *A. karelinianus*, in the rocky alpine steppes of Chelyabinsk Province, on Eremikha and Karavai Mts. near the city Vishnevogorsk, on Egoza Mt. near the city of Kyshtym, and in Bashkir ASSR near the village of Bikkuzino; for *A. helmii*, on rocky alpine steppes on Kushtau Mt. in Bashkir ASSR near the city of Sterlitamak and in Orenburg Province near the city of Guberlya; for *A. clerceanus*, on granite crags in Sverdlovsk Province at Severka and Palkino stations in the vicinity of Sverdlovsk,

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0096-7807/84/1503-0103$08.50 © 1985 Plenum Publishing Corporation

Fig. 1. Age states of *A. karelinianus*: pl) plantules, j) juvenile, im) immature, g_1) young generative, g_2) mature generative, g_3) old generative, s) senile.

and also near Iset' station at Chertovyi Gorodische; and at the sole habitat of *A. kungurensis* in Perm Province on the gypsum Mt. Podkamennaya along the Sylva R. near the city of Kungur. Abbreviated names for the populations according to their geographic position (Eremikha, Guberlya, etc.) are subsequently used in the paper. All populations studied have in some measure been subjected to anthropogenic influences (livestock grazing, berry collection, recreation, etc.).

Population structure was studied in natural habitats on 10 × 10 m sample areas. The characteristics of the various age states (Uranov, 1975) of the species selected were first clarified. Then all individuals of the given milk vetch species were counted on each sample area with distribution into age groups. Each plant was marked, and its position entered on a schematic map. In later years the appearance of young specimens, the passage of individuals from one age state to another, and the death of individuals were noted on the same sample areas. On this basis the long-term dynamics of the population age structure against the background of anthropogenic effects was clarified. In addition to field studies, observations were made of the development of plants cultivated from seeds at the Botanical Garden of the Institute of Plant and Animal Ecology, Ural Scientific Center, Academy of Sciences of the USSR. This made it possible to refine the characteristics of the early milk vetch age states (from plantules to immature individuals).

All milk vetch species we studied belong to the shrub life form, producing a multiheaded stem—root, the caudex. These are vegetatively immobile plants, reproducing only by means of seeds.

Astragalus karelinianus

The root in the plantules of this milk vetch is slightly branched and up to 6 cm long (Fig. 1). The cotyledons are located at the soil surface or somewhat (0.5 cm) higher. After the cotyledons the supracotyledonous shoot appears, bearing up to three primary ternately complex leaves. The plants are no more than 2 cm high.

The plants enter the juvenile state at the end of the first growing season. The primary root is more developed, up to 9 cm long, and up to 1.5 mm in diameter at the root collar. The stem is single and about 5 cm high; the leaves at first are ternately complex and then imparipinnately complex (with two to three leaflet pairs). The cotyledons die with the appearance of the imparipinnately complex leaf. Buds are formed in the cotyledonary sinuses.

Upon the transition to the immature state the root elongates and branches slightly. The formation of a caudex commences: Lateral plagiotropic shoots with ascending apices arise from the buds established in the cotyledonary sinuses. The lower part of the annual shoots lignify. Due to the pulling action of the root, the cotyledonary node along with the bases of the lateral shoots is submerged into the soil to a depth of up to 1 cm. The shrubs are 5-7 cm high and are densely leaved. The number of leaflet pairs per leaf increases to four to seven.

A stout, highly branched caudex (2-3 cm in diameter with up to seven heads) is formed during the generative stage of life of the plants. The root reaches 0.8-1.2 m length and is

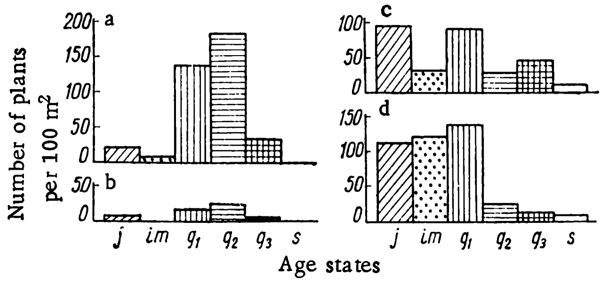

Fig. 2. Age structure of *A. kareliniamus* populations. Populations: a) Eremikha, 1976, 370 plants; b) Karavai, 1979, 48 plants; c) Egoza, 1979, 297 plants; d) Bikkuzino, 1977, 415 plants per 100 m^2.

highly branched in old plants. The lignifying, perennial part of the shoots is 10-15 cm long. The leaflets number seven to eight. The number of caudex heads and the number of dead heads increase upon the transition of plants from young to mature and then to old generative plants. Foilage density declines with age. The shrubs reach 30-50 cm height and 50-80 cm diameter. Up to 10 inflorescences with 1-3 flowers develop in young generative plants; up to 50 inflorescences with 6-7 flowers in mature generative plants; the number of inflorescences declines to 10-12 in old generative plants.

The foilage is very weak in senile plants. The caudex is thickened with many dead heads. All shoots are vegetative; no flowers are formed.

Comparison of the age spectra of four *A. kareliniamus* cenopopulations (Fig. 2) shows that they all belong to the normal (Uranov, 1975) or homeostatic category (Rabotnov, 1983). The Egoza and Bikkuzino populations are complete, while the Karavai population (1979) lacks immature and senile plants and the Eremikha population (1976), senile plants. The density of most populations is 300-400 plants per 100 m^2; only in the Karavai population is it sharply depressed (to 48 plants per 100 m^2) as a result of intensive livestock grazing and trampling. The Eremikha and Karavai populations are transitional from young to mature, and the remaining populations are young.

All populations examined are experiencing anthropogenic influences and are at various stages of recovery after disturbances. Judging by the large fraction of immature plants, the recovery of the Bikkuzino population is proceeding most successfully. The Karavai population, on a mountain slope near Vishnevogorsk, has suffered quite severely, indicated by its low density and the incomplete age spectrum (absence of immature and senile plants). This population is recovering slowly and weakly; its very existence is threatened.

The long-term dynamics of the *A. kareliniamus* populations can be judged by the Eremikha population, observed in 1976, 1978, 1979, and 1983 (Fig. 3). Eight years before the start of the observations, in 1968, pine was planted on the volcano Eremikha in plow furrows, which was accompanied by the partial destruction of the plant cover. The exposure of the substrate favored an invasion of *A. kareliniamus* onto the areas free of vegetation and the enhancement of its fraction within the alpine steppe community. A normal, incomplete population had formed here by the start of the observations (1976). After two years, in 1978, it acquired the features of a typical mature complete population (senile plants appeared). In 1979 the population passed to thecategory of old populations and again became incomplete, but this time due to the absence of immature individuals. In 1983 it remained an old, incomplete population, but now it also lacked juvenile plants.

The population density from 1976 to 1979 was maintained at approximately the same level (343-370 individuals per 100 m^2), but in 1983 it declined to 114 individuals per 100 m^2. Thus, at the end of the observation period the recovery of *A. kareliniamus* had been impaired and its population was undergoing extinction in connection with an increase in the density of the herbaceous cover and increasing competition on the part of steppe sod grasses.

Astragalus helmii

The plantule root develops more rapidly than the stem, is 6-8 cm long, and unbranched. Near the soil surface are two cotyledons and a supracotyledonary shoot with several simple leaflets. The plants are 2.5-3 cm high.

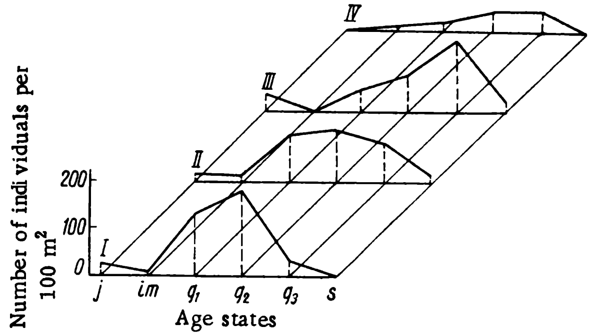

Fig. 3. Dynamics of age structure of Eremikha population of *A. karelinianus*: I) 1976, 370 plants; II) 1978, 356 plants; III) 1979, 343 plants; IV) 1983, 114 plants per 100 m^2.

The root in juveniles reaches 8-10 cm length, is weakly branched, and 0.6-1.5 mm in diameter. The stem is 3-4 cm high, unbranched, and at first bears several simple leaflets, followed by ternately complex leaves.

The root in the immature state is more stout, is 12-15 cm long and 1.5-2 mm in diameter, and has numerous second and third order branches. A caudex (with three to five heads) forms at this time. The leaves are for the most part ternately complex, partially imparipinnate with two pairs of leaflets.

The root in young generative individuals is 15-20 cm long, 2-3 mm diameter and is highly branched. The caudex is well developed with numerous lateral plagiotropic rising shoots. Upon the transition to the mature state the root elongates to 30 cm and branches to the fourth order. The caudex is 7-8 cm in diameter and strongly branched. In older generative individuals the caudex is 12-15 mm in diameter and the degree of its branching increases still more. The perennial parts of the shoots reach 5-6 cm length, and many dead shoots are present. The leaves are imparipinnate; three to four leaflet pairs are usually present in the complex leaf of young and mature plants and two to three in old generative plants. *A. helmii* begins blooming during the second half of May. Sometimes a secondary blooming is observed in July or August. The flowers are solitary or in an oliganthous raceme. Young plants have up to three flowers per raceme; mature plants, up to six flowers; generative function is absent in old plants. The bushes of generative plants are 15-20 cm in diameter and 14-18 cm high.

The caudex in senile plants is about 2 cm in diameter, and some of its heads die and are destroyed. The root is 40-50 cm in length and branches to the fifth order. The lateral branchings of the root are 3-4 mm in diameter. The lignified parts of the shoots reach 7-8 cm in length at a diameter of 4-6 mm. The young shoots are shortened and arise in bundles from quiescent buds on the lignified parts of the stem. The leaves are primarily ternately complex and some are simple. The bushes are branchy, little lignified, and short with numerous dead shoots. Generative function is lost. Senile plants live two to three years and then die.

Judging by the age spectra (Fig. 4), both *A. helmii* populations studied are normal complete populations. The generative group in the Kushtau population near Sterlitamak is suppressed, and its composition is dominated by old plants. There are many dying senile plants. The proportion of juvenile and immature plants is very large. The spectrum reflects the replacement of a descending wave (die-back) by an ascending (recovery).

The Guberlya population in 1976 was young and dominated by young generative plants; the role of juvenile and immature plants was quite large. The cold and dry spring of 1979 (snow fell on April 20, while the first rain fell on June 2) had a significant influence on the state of this population (Fig. 5). There was a mass die-back of plants of all age groups, and the population density declined appreciably compared with 1976. The population was incomplete in 1979, since the senile plants fell out. After four years, in 1983, the population took on the features of an old population and was dominated by old generative and senile plants. However, the presence of juvenile and immature plants indicates that even in this case the descending wave was succeeded by an ascending. Apparently, both populations are recovering quite successfully in spite of anthropogenic influences.

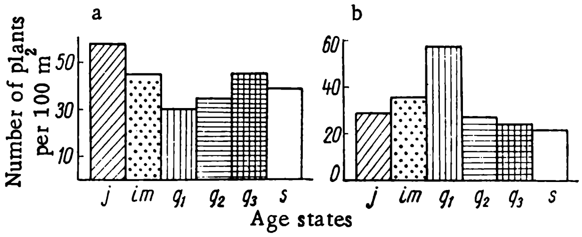

Fig. 4. Age structure of *A. helmii* populations. Populations: a) Kushtau, 1977, 251 plants; b) Guberlya, 1976, 185 plants per 100 m².

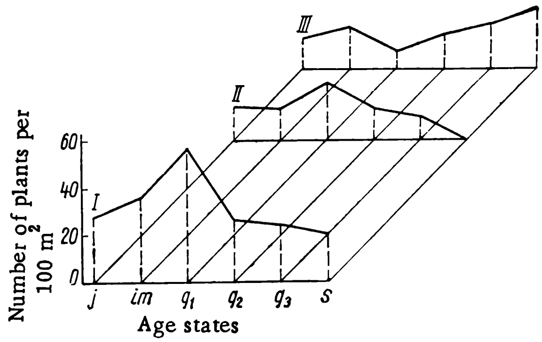

Fig. 5. Dynamics of age structure of *A. helmii* Guberlya population: 1) 1976, 185 plants; II) 1979, 75 plants; III) 1983, 99 plants per 100 m².

Astragalus clerceanus

The plantules have an unbranched root of up to 3 cm long. At first there are a pair of cotyledons and a supracotyledonary shoot bearing one ternately complex leaf; later one to two imparipinnately complex leaves form (usually with two pairs of leaflets).

The root of juvenile plants is weakly branched, about 10 cm long, and 0.5-0.7 mm in diameter. The stem is elongated, and several imparipinnately complex leaves (with three to five leaflet pairs) appear on it. Buds are established in the cotyledonary sinuses, while the cotyledons themselves turn brown and die. The plants reach 5-6 cm in height.

The immature plants have a longer (13-15 cm) branched root of 1-1.2 mm in diameter. The leaves are imparipinnate with four pairs of leaves. Plagiotropic shoots (at first with ternate leaves) appear from the buds established in the cotyledonary sinuses; caudex formation begins. The plants are up to 10-12 cm high.

The root is still more developed in plants in the generative state and is 15-20 cm long and branched. The caudex is 3-4 mm in diameter with three to four heads; the bases of dead shoots are retained on its apex. The bush is open, 30-50 cm in diameter, and 16-20 cm high. The lateral shoots are extending and ascending. The leaves have four to seven leaflet pairs and one unpaired leaflet. Each inflorescence contains up to 12 flowers. With the transition from the young generative state to the mature and old states the caudex thickens, and the number of its branches and dead shoots increases.

Senile plants are poorly leaved with numerous dead heads and the remains of dead shoots.

The life-span of *A. clerceanus* is shorter than that of the other species from this genus that we studied. Ontogenesis under natural conditions lasts about seven years. The plants die earlier, during the third year of life, when cultivated in a botanical garden. The transition from one age state to another occurs rapidly. Many plants die as early as in the old generative state, which lasts one to two years; only a few plants pass to the senile state.

The Chertovo Gorodishche and Palkino populations (Fig. 6) are normal incomplete young populations; the first lacks not only senile but also juvenile plants. The Severka popula-

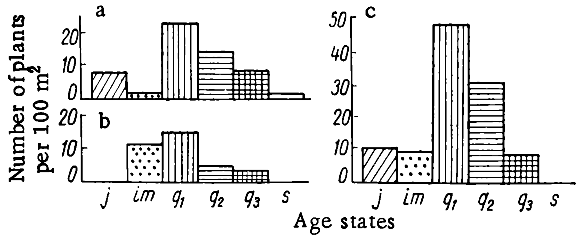

Fig. 6. Age structure of *A. clerceanus* populations. Populations: a) Severka, 1979, 57 plants; b) Chertovo Gorodishche, 1979, 35 plants; c) Palkino, 1979, 100 plants per 100 m².

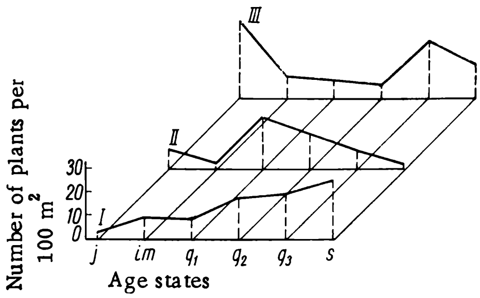

Fig. 7. Dynamics of age structure of *A. clerceanus* Severka population: I) 1977, 86 plants; II) 1979, 57 plants; III) 1983, 98 plants per 100 m².

tion is a normal complete population. It completed its transition to the old state in 1977, and there were many senile plants. However, after just two years, in 1979, the die-back of the old generation was completed and the population passed to the young category (Fig. 7). The die-back of the old generation in the population was completed in 1983, but there were many juvenile and immature plants. This indicates a rapid succession of population waves in this milk vetch species. The population density did not change appreciably during the observation period.

Astragalus kungurensis

This is a rare, critically endangered species growing at the foot of Podkamennaya Mt. on the lower part of the steep southern bank of the Sylva R., which is covered by steppified pine forest. Podkamennaya Mt. is composed of gypsum, and the relief is of the karst type. Karst cones intercept a significant portion of the surface runoff. The unique combination of edaphic and climatic factors (the easily disturbed, mobile, continuously exposed substrate, alkaline pH, abundance of lime, intensity of illumination, good warming of the surface) was responsible for the preservation of the endemic milk vetch species in the form of a single population at this site in open glades and pine-forest edges. T. P. Belkovskaya (1978) points out that the *A. kungurensis* population numbered about 500 plants in 1976. According to our data, approximately 400 plants grew here in 1980, while their numbers declined to approximately 300 plants in 1983 after strong rains causing severe erosion of the slope surface.

A. kungurensis plantules have a thin (0.2-0.3 mm diameter) unbranched root of 3-5 cm length. The hypocotyl is partially submerged into the litter and is 2-4 cm long. The cotyledons are well developed and rather large. The epicotyl is in the form of a small paripinnate leaf (with two pairs of leaflets).

The root in juvenile plants is 12-15 mm long and 0.4-0.6 mm in diameter. Two leaves, imparipinnate or ternate (with two leaflet pairs), usually rise above the dead cotyledons. The plant is up to 5 cm high.

The root of immature plants is 2.5 mm in diameter, 15 cm long, and unbranched. The belowground stem (caudex rudiment, which is still unbranched and straight), about 3 cm long and 3-4 mm thick, is covered by the remains of old petioles and stipules. The leaves are imparipinnate with six to seven leaflet pairs.

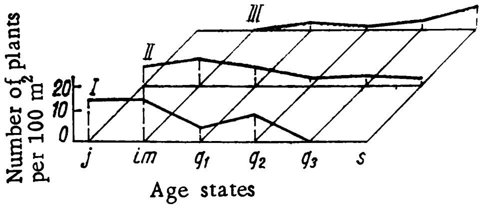

Fig. 8. Dynamics of age structure of *A. kungurensis* Podkamennaya population: I) 1980, 45 plants; II) 1982, 36 plants; III) 1983, 15 plants per 100 m^2.

The root of generative plants is 1-1.5 m long and about 1 cm thick. The caudex is 1.5-2 cm in diameter with four to six heads. The leaves are imparipinnate, and young plants have 5-10 leaflet pairs, mature plants, 10-19, and old plants, 10-24. The shrub is 18-30 cm high and 20-30 cm in diameter. Two to three flower stalks form in young plants, six to eight in mature, and two to four in old. The number of flowers per inflorescence reaches six.

Senile plants are poorly leaved; the caudex is multiheaded and bears a large number of remnants of dead shoots.

The dynamics of the population age structure can be judged by Fig. 8. In 1980 the population was a normal incomplete population (senile plants were absent), transitional from young to mature. In 1982 it became complete, and senile plants appeared due to a decline in the number of mature and old generative plants. In 1983 the population again became an incomplete dying population, senile plants were dominant and juvenile and immature plants were absent, while generative plants were present in negligible number. The population density declined during the observation period from 45 to 15 plants per 100 m^2.

CONCLUSIONS

1. The milk vetch species endemic to the Urals and the Cisural Area (*A. karelinianus, A. helmii, A. clerceanus, and A. kungurensis*) belong to the life form of shrubs producing a caudex. The type, form, and size of the leaves, the degree of development and fragmentation of the caudex, the relative numbers of live and dead shoots, and the reproductive potential all change during the ontogenesis of these plants, making it possible to distinguish age states precisely and to elucidate the age structure and long-term dynamics of the populations.

2. All milk vetch species selected for study are vegetatively immobile plants reproducing only by means of seeds and are erosion-lovers that grow on rocky alpine steppes and crags, where competition from other plants (mainly sod grasses) is attenuated and the substrate is continuously renewed and exposed as a result of substrate weathering, the displacement of blocks down the slope, and water and wind erosion. Their reproductive strategy amounts to a rapid seizure of bare fine-earth regions free of vegetation appearing as a result of erosion or the action of ungulates and man. This feature makes possible the long existance and survival of small (with respect to the number of plants) populations of endemic milk vetches on a limited area, in places where this is favored by the edaphic conditions (rocky steppe slopes, and crag exposures within the forest subjected to water erosion).

3. Endemic Ural milk vetches exist in the form of small populations isolated from one another by geographic, phytocenotic, or phenologic barriers. Their populations are normal (homeostatic), complete, or incomplete. These species are characterized by wave-like population dynamics with an alternation of bursts and wanings of recovery processes, which is due to the simultaneous transition of a large number of plants from one state to another. The massive die-back of plants of all age groups is observed during years with unfavorable weather conditions. The duration of population waves differs in different species (shorter in *A. clerceanus* and longer in the other species studied), which is related to the varying duration of ontogenesis. Anthropogenic effects (recreation, livestock grazing) cause a decline in population density and an increase in the frequency of population waves.

4. In spite of the small size of the individual populations of endemic milk vetches and their frequently great distance from one another, they usually withstand moderate anthro-

pogenic effects (livestock grazing, recreation) and recover quite successfully. Nevertheless, the number and size of the populations are declining with the increasing levels of anthropogenic loads and the destruction of milk vetch habitats, which may result in the complete extinction of these rare species. Particularly alarming is the fate of *A. kungurensis*, which exists in the form of a single population and whose numbers have recently declined to approximately 300 plants.

5. Endemic rocky alpine steppe milk vetches should be specially protected at characteristic growth sites. However, the complete exemption of such sites from economic utilization (reserves) cannot assure the protection of the small populations of these rare plants. Their most favorable regimen is not a reserve but moderate, regulated use (grazing in steppe habitats and recreation in crag habitats). To promote the seed renewal of the endemic plants of this group in habitats where erosive processes are attenuated, it is desirable occasionally to clear the soil surface of sod grasses at separate sites. The monitoring of the state of the populations both of endemic milk vetches and other rare and disappearing plants must be organized.

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