

Handbook of vegetation science

The population structure of vegetation

Edited by J. White

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М. Работнов

This book is dedicated to the distinguished Soviet geobotanist
Professor T. A. RABOTNOV

His researches on the demography of plant coenopopulations have been
its inspiration.

POPULATION BIOLOGY OF STEPPE PLANTS

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ABSTRACT

Five types of life history are distinguished among herbaceous species growing in steppe grasslands in Kazakhstan: they include tussock plants, tap-rooted plants of various kinds and long-rhizome herbs. They vary in the structure and dynamics of their coenopopulations and in the extent to which they are maintained in coenoses by seed or by vegetative growth. An understanding of the morphology and ontogenetic development of plants in natural coenoses is an indispensable prerequisite for describing their coenopopulation characteristics. These in turn reveal how plant communities are organised as dynamic systems.

INTRODUCTION

The existence of multispecies communities is possible because the species of the community are ecologically and biologically unique (Ramenskii 1925, Golubev 1959, 1970). The demographic characteristics of species ensure the segregation of their ecological attributes in time and space (Harper 1977, Grubb 1977), so that individual plants use the environmental resources in a complementary fashion (Ramenskii 1925). Although the totality of life history characters of populations is unique in each species, a considerable similarity and overlap of several features among different species cannot be ruled out. Such differences and similarities allow us to differentiate several types of life history attributes (see review by Harper 1977). These are commonly based on the reproductive biology of species and on the division of resources between reproductive and vegetative organs. Ramenskii (1938) seems to have been the first to initiate a functional typology of plant behaviour and to specify three phytocoenotypes known as 'patients', 'violents' and 'explerents'. The contemporary concepts of types of plant 'strategy' (Grime 1978), correspond on the whole to Ramenskii's ideas.

Studies of coenopopulations of perennial herbs in different coenoses (Smirnova et al. 1976, Uranov et al. 1977) and the review of literature by

Harper (1977) seem to suggest that a behavioural typology of perennial herbs is possible. The main characters used for differentiation of various types must be relevant to and decisive for the continued existence of a species in a coenosis and help to identify and determine its role in the community. In our opinion, such characters are: 1. The life-form and the course of plant ontogenesis; 2. The manner of species self-maintenance in a coenosis, that is, the relationship between the type of vegetative propagation and the frequency of seed reproduction; 3. Duration of ontogenesis; 4. Intensity of plant mortality during ontogeny.

In this paper we confine our attention to steppe plants and according to the characteristics listed above, we differentiate the following types of life history in these plants: (I) tussock plants, (II) tap-rooted perennial plants with seed self-maintenance, (III) tap-rooted perennial plants with 'mixed' self-maintenance, (IV) tap-rooted plants with a short duration of ontogeny, (V) long-rhizome herbs.

STEPPE GRASSLANDS

The steppe environment

Our material was collected in Naurzum Preserve (North Kazakhstan), located in the subzone of dry steppes. The dry steppes ('tussock-grasslands' of Lavrenko 1954) stretch in latitude from the Black Sea to the Baikal Region. They are confined to southern chernozems and chestnut soils with a very deep underground water table. The dry steppe region is characterized by a continental climate with hot dry summer and cold winter. The average annual rainfall is 260–300 mm. Although maximum precipitation falls in summer, air humidity and soil moisture content decrease significantly in this period because of higher temperature and evaporation. The dry period falls between June and September, but in some years it is less pronounced. The arid climate is the basic factor determining plant characteristics in this zone. In spite of the considerable geographical extent and ecological heterogeneity of dry steppes they have a number of common characteristics: predominance of tussock grasses of the genera *Stipa*, *Festuca*, *Koeleria*, *Agropyron* (Lavrenko 1940); low floristic diversity of communities; discontinuous overground plant cover; atmospheric water supply; lack of forests.

In Naurzum Preserve the investigations were conducted on sandy soils. These psammophyte variants of zonal steppes are reported in different regions of North Kazakhstan (Karamysheva and Rachkovskaya 1973).

Vegetation

Stipa pennata, *Festuca beckeri* and in places *F. valesiaca* (subsp. *sulcata*) provide the predominant cover; *Koeleria glauca*, *K. macrantha*, *Phleum phleoides* occur continuously but in low abundance. Of the various perennial herbs, *Potentilla cinerea*, *Centaurea sibirica*, *Artemisia campestris*,

Onosma simplicissimum occur most continuously. Annual plants are limited to *Bassia sedoides*, *Coryspermum hyssopifolium*, *Polygonum ar-
enarium*. The number of species reaches 40–44 per 100 m². The total projective cover varies from 50% to 80%. The plants were studied in one particular phytocoenosis; all individuals of each species in that phytocoenosis were collectively regarded as a 'coenopopulation'.

AGE-STATE ANALYSIS OF COENOPOPULATIONS

Numbers and age structure are the most essential coenopopulation parameters. The investigation of age structure in perennial herbs is rather difficult since the calendar age can be determined in only few cases. In our studies we used the concept of age-states developed by T.A. Rabotov and other Soviet botanists. Age-states are the successive stages of ontogeny of a genetic individual (see Gatsuk et al. 1980 for a review). The individual plant is characterized by morphological integrity and it may be of seed or vegetative origin. A vegetatively derived individual is given the name 'particule'. On the basis of morphological characters the following age states and corresponding groups of individuals are differentiated (with their standardised abbreviation): seeds (**se**); seedlings (**pl**); juvenile (**j**); immature (**im**); virginile (**v**); reproductive, young (**g₁**), mature (**g₂**), and old (**g₃**); subsenile (**ss**) and senile (**s**). Investigations of age-state structure must be based on a clear understanding of plant morphology, to enable one to recognize the individual unit and the changes during its ontogeny.

The following four systems of 'calculation units' are used for enumerating of plants in coenopopulation studies (with the age-state categories in brackets), illustrated in Fig. 1.

- I Individuals of seed origin during the whole ontogeny;
- II Individuals derived from seeds (**j-g₁**), compact clones (**g₂**, **g₃**, **ss**) or single particules (**s**). Since a single particule may be considered as a residue of a formerly existing clone, this second system of calculation units corresponds to the enumeration of genets in Harper's (1977) sense;
- III Individuals of seed origin (**j-g₁**), clones (**g₂**), particules within the clones (**g₃**, **ss**, **s**) or single particules (**s**).
- IV 'Partial tufts' or shoots within one or different individuals. A partial tuft (Serebryakov 1962) is a cluster of shoots with its own roots, connected with the same tuft by long rhizomes. Particules and partial tufts and shoots seem to correspond to ramets (Harper 1977).

The different types of calculation units reflect the various degrees of shoot concentration in plants of different life-forms. The autonomy of shoots and the morphological integrity of the plant as a whole change during ontogeny. The shoots may all be concentrated in one place, or they may be dispersed in several clusters linked to one another. The centre of shoot concentration is regarded as the source of a plant's phytocoenotic influence. As a consequence two types of calculation unit are distinguished by us, a morphological unit and a phytocoenotic unit. The former corre-

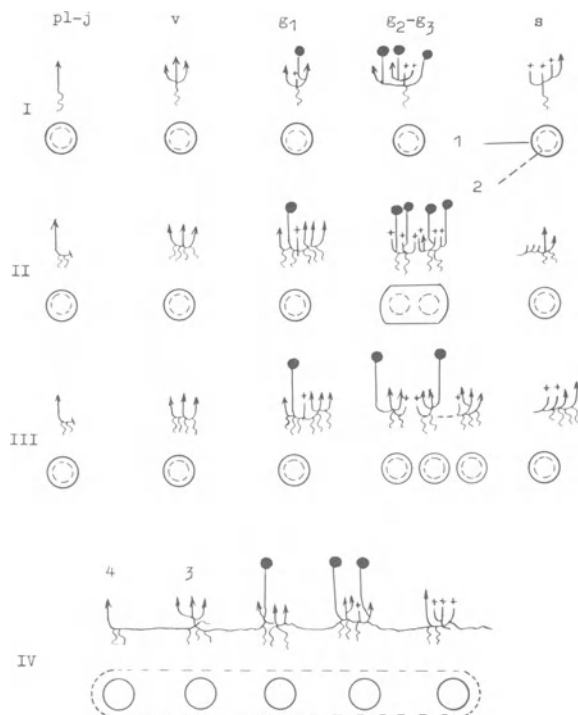


Fig. 1. Calculation systems used in studies of plant coenopopulations. Two types of units are distinguished, phytocoenotic (1) and morphological (2) (see text). I: Both types are coincident during the entire ontogeny and are of seed origin (genets). II and III: The units are distinct at later stages of ontogeny; morphological units may remain closely united to give a single phytocoenotic unit (II) or may fragment to give separate particles, each of which becomes an independent phytocoenotic unit (III). IV: A morphological unit, while retaining physical integrity may behave as multiple phytocoenotic units, each consisting of a partial tuft (3) or shoot (4).

sponds to the individual as a morphological and physical entity, the latter to the centre of shoot and root concentration. The correlation between the two units is different for various life forms and is determined by careful mapping and excavation of plants in natural phytocoenoses (Fig. 1).

System I is used for tap-rooted perennials, systems II and III for tussock grasses and species with short-rhizomes and system IV for species with long-rhizomes and those with root suckers.

The total plant number (in terms of calculation units) and the percentage of calculation units of different age-state groups (age spectra according to Uranov 1967) are determined usually on small plots ($0.25-1 \text{ m}^2$) placed by a random-regular method (Vasilevich 1969) within a uniform area of a phytocoenosis. In our studies the number of such plots ranged from 20 to 160 for each species. Most observations were carried out at permanent transects ($0.5 \times 10 \text{ m}^2$) where the positions of plants were mapped annually, once a season in June.

The seed and fruit numbers of all flowering individuals were estimated on permanent $1 \times 10 \text{ m}^2$ transects. The number of seedlings was determined not less than twice a season on either permanent or nonpermanent plots, forming a $0.2 \times 10 \text{ m}^2$ transect. Seedlings are usually not recorded in the estimations of age-state spectra because of their ephemeral existence: a great number of seedlings die off in the first months of life, and those that survive pass on to the next age-state.

TYPE I – TUSsock PLANTS

The life history features discussed in this section are typical of:

- (a) firm and loose tussock grasses, for example, *Stipa lessingiana*, *S. sareptana*, *S. pennata*, *S. rubens*, *S. capillata*, *Festuca valesiaca*, subsp. *sulcata*, *F. beckeri*, *Cleistogenes squarrosa*, *Koeleria macrantha*, *K. glauca*, *Phleum phleoides*, and
- (b) herbs with short-rhizomes, for example, *Potentilla cinerea*, *Centaurea sibirica*, *Arenaria procera*.

The species of *Stipa* and *Festuca* are usually the dominants of steppe communities. The rest of the grasses are, as a rule, in a subordinate position although they may become dominants in some geographical and ecological steppe types: for example, there are steppes with predominance of *Cleistogenes squarrosa* in the Transbaikalian Region and in Mongolia. In the arid steppes herbs with short-rhizomes are, as a rule, only moderately abundant, but are permanently present in the community.

Self-maintenance of coenopopulations of these species is by seed. At a certain stage of ontogeny the seedling transforms itself to a clone by vegetative propagation. An adult individual of seed origin is a more or less compact shoot system with regeneration buds at the base of shoots, and each shoot has its own root system. The death of shoots in the centre of the individual fragments it into particules. However, the particules are not rejuvenated after separation, as a rule, and ageing processes result in their death. This vegetative growth cannot provide prolonged existence of the species in a given habitat in the absence of regeneration by seeds, although the longevity of seed-derived individuals and of clones in these species may be considerable, from 30 to 80 years. More detailed life-history characteristics are given separately for the two groups of species.

Firm-tussock grasses

Seeds and seedlings

Steppe tussock grasses are characterised by seed regeneration whose efficiency depends on (a) potential and actual seed productivity, (b) seed germination capacity, (c) seed bank in the soil and (d) survival of seedlings and juvenile plants. 'Potential seed productivity' is defined as the number of ovules formed per plant; 'potential seed yield' is the number of ovules per 1 m^2 . 'Actual seed productivity' is defined as the number of healthy

Table 1. Potential and actual seed yields in some firm-tussock grasses in the Naurzum Preserve.

Species	Year of observation	Number of flowering plants per 10 m ²	Number of reproductive shoots per 10 m ²	% Caryopses		Seed yield per 1 m ²		
				Healthy	Damaged	Puny	Potential	Actual
<i>Stipa pennata</i>	1973	22	26	19.8	54.0	26.2	24.4	4.7
	1974	50	129	64.8	29.5	5.7	92.0	54.9
	1975	27	64		No data		66.1	No data
	1976	9	15	36.9	0	63.1	13.0	4.9
	1977	34	93	60.7	32.2	7.1	83.3	50.6
<i>Festuca beckeri</i> *	1973	2	2	23.4	17.4	59.2	18.4	4.3
	1974	2	2	9.3	55.0	35.7	12.9	1.2
	1975	2	4	17.0	28.6	54.4	24.1	4.1
<i>Koeleria macrantha</i> *	1974	3	6	4.7	85.3	10.0	55.7	2.6
	1975	3	4	8.3	83.6	8.1	66.4	4.8

*In these species reproductive shoots were absent in 1976 and 1977.

seeds per plant; 'actual seed yield' is the number of healthy seeds per 1 m^2 .

The limits of potential seed productivity are genetically fixed, and specific for each species and habitat. In sandy steppes the value is 10–30 ovules per plant in *Stipa pennata*, 60–120 in *Festuca beckeri*, 180–200 in *Koeleria macrantha*. The number of healthy (intact) seeds formed depends on pollination conditions and the degree of ovary damage caused by phytophagous insects. Firm-tussock grasses are all wind-pollinated. For many species of *Stipa* and *Festuca* different rates of cleistogamy have been reported: it is unevenly pronounced in different species and varies within one species in different years (Ponomarev and Zvorygina 1949, Solntseva 1968). Cleistogamy increases under poor flowering conditions (excessive rain or drought for example). Many species of *Stipa* are characterised by rapid ripening of seeds in pollinated flowers and by non-simultaneous ripening in different parts of the inflorescence, which prolongs flowering and seed ripening (Solntseva 1968). These seed development characteristics may be considered as adaptations to the rather changeable spring conditions in the subzone of dry steppes.

The development of phytophagous insects and parasitic fungi in the reproductive parts of steppe grasses is a typical phenomenon. The reproductive shoots of *Stipa pennata* are damaged by rust fungi; the ovaries are eaten by gallfly larvae, tripsids and aphids. Tripsids are significant pests in *Festuca beckeri* and *Koeleria* species. Inflorescence predation and poor pollination may result in extremely poor actual seed yield, from 4 to 60% of the potential level; this varies considerably from year to year (Table 1).

The seed yield depends not only on the level of potential seed productivity but also on the number of flowering plants in the coenopopulation and the number of reproductive shoots on each flowering individual; the fluctuations of these parameters will be mentioned later. In *Stipa pennata* coenopopulations a rather high actual seed yield is developed, in spite of the relatively low potential seed productivity (Table 1). In this species the percentage of healthy seeds was highest compared to other grass species. It seems to be one of the reasons ensuring the predominant role of *Stipa pennata*. The subordinated position of *Koeleria macrantha* in the community investigated is primarily related to the fact that an insignificant number of healthy seeds is formed on the plant (Table 1), although the species showed high levels of potential seed productivity. The potential seed productivity of steppe grasses is, as a rule, stable, while the actual productivity changes considerably according to the phytocoenotic conditions and regime of economic activities (Osychnyuk and Shupranov 1978).

Caryopsis dispersion of most steppe grasses (*Festuca*, *Koeleria*, *Agropyron*) is by barochory (Levina 1956). In *Stipa* the seeds are wind-dispersed, but even with strong wind they are not usually carried further than 3–4 (rarely 11) m (Ponomarev and Zvorygina 1949). The fate of the fallen fruits is different: some caryopses are retained in the litter and a great number of them are eaten by rodents or damaged by phytophagous insects. Less than 3% of *Stipa* caryopses falling on the ground are

Table 2. Seed bank of some grasses in the soil of Central Kazakhstan steppes in vegetation of *Stipa lessingiana* + *Festuca valesiaca* + *Artemisia gracilescens* (Borissova and Popova 1972).

Species	Year	Seed stock (no. m ⁻²) in soil layers				
		0–2 cm	2–4 cm	4–6 cm	6–8 cm	8–10 cm
<i>Stipa lessingiana</i>	1960	140	80	0	0	0
	1961	50	19	14	0	0
<i>Festuca valesiaca</i> subsp. <i>sulcata</i>	1960	300	100	80	80	0
	1961	1133	128	50	43	11

transformed into viable seedlings (Ponomarev and Zvorygina 1949). Evidently at this stage of ontogeny the death rate is the highest. *Stipa* caryopses become submerged in the soil to a depth of 2–4 cm owing to its 'screwing-in' mechanism. In *Festuca* and *Koeleria* the caryopses germinate directly on the soil surface: this factor increases the risk of death in seedlings of these species in the first stages of development and determines the subsequent tussock position. The seeds of many species of *Stipa* are characterised by inherent dormancy of different duration: some may germinate after nine or even 16–17 years dormancy in laboratory conditions (Bespalova and Borissova 1979). The germination capacity and the onset of germination in caryopses change according to the time of ripening, depending on the meteorological conditions in the year of fruit ripening (Bespalova and Borissova 1979). Because of the long retention of viability a seed bank can be developed in the soil. In grasses growing in communities on loamy soils the seed bank is rather large and can vary significantly from year to year (Table 2). Of the total seed number found in soil, the live caryopses of *Stipa lessingiana* and *Festuca valesiaca* represented 7% and 58% respectively (Borissova and Popova 1971). According to our observations, there is practically no seed reserve of most species in sandy steppe soil. The seeds of the current or previous year are the basic source of regeneration. In some years seedlings appear only on account of the seed reserves in the loamy soil of the steppes.

Steppe plant seedlings appear rather sporadically (not annually) according to moisture conditions. The seeds of most grass species germinate both in spring and autumn, but *Stipa* only in spring. Seedling number reaches 6–8 per 1 m² in sandy steppes. If the seedlings appear in spring most of them (50–84%) die in the course of the summer. Thus even in the dominant grasses the number of juvenile plants is rather low (2–6 per 1 m²).

Age-state ontogeny

Ontogenetic development and morphological changes of individuals reflect the plant's life form. Ontogeny is rather similar in different species of firm-tussock grasses (Fig. 2, see also Gatsuk et al. 1980). The uniaxial juvenile plant passes into the virginile state, as a result of shoot tillering

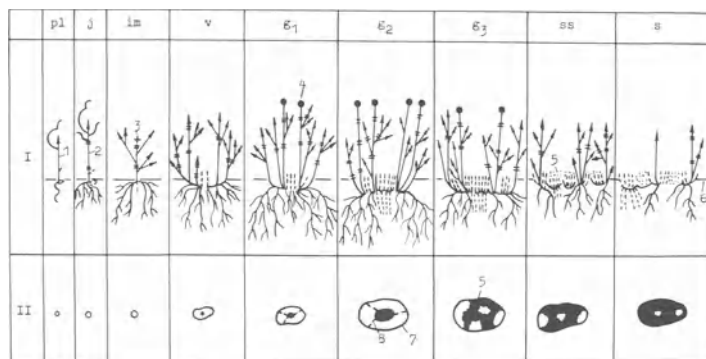


Fig. 2. Age-states in firm-tussock grasses (for example *Festuca beckeri* from Mikhailova (1977)). I, schematic diagram of tussock ontogeny; II, horizontal tussock projection. 1, vegetative first year shoot with leaves; 2, vegetative perennial shoot; 3, dead shoot; 4, reproductive shoot; 5, dead part of a tussock; 6, soil level; 7, boundary of an individual of seed origin or of the clone (genet); 8, boundary of the particles, the individuals of vegetative origin (ramets).

and forms a tussock. Then it begins to flower (g_1). Shoot tillering becomes more intensive, the tussock increases, but simultaneously dead shoots accumulate (g_2). The tussock divides into particles which together compose a clone. The ageing processes in shoot and root systems are intensified, the frequency of shoot formation is reduced, the number of live shoots declines (g_3 , ss). Tussock ageing results in a reduction of live shoot number to 2–3, and eventually only one particle remains from the clone (s).

The difference in ontogeny between the species of dense-tussock grasses is due primarily to the different durations of each age-state: these can be established approximately by using the methods of calendar age determination (Persikova 1959, Bedanokova et al. 1975). Life-span varies under different conditions (Table 3), increasing usually in unfavourable conditions. In some species (*Koeleria glauca*, *K. macrantha*) the longevity of clones in Naurzum Preserve may reach 100 years. In firm tussock grasses the old age period ($g_3 + ss + s$) is the longest. In many natural communities the age-state structure of coenopopulations is determined by this peculiarity. There are cases, however, when the old age period is greatly reduced, and the senile state is less evident, as reported for *Stipa lessingiana* and *Festuca valesiaca* in Central Kazakhstan steppes (Borissova and Popova 1971). The pre-reproductive period is usually extended in grasses of natural communities. It is significantly reduced in culture, where *Stipa* species for example flower in the second year of life (Ivashin and Chuprina 1976).

Firm-tussock grasses are generally characterised by a considerable life-span which can be considered as an adaptive character. In subarid and arid conditions this guarantees a stable species position even with relatively low actual seed productivity. In many species the tussock constitutes a clone in the mature state and with ageing the particles becomes more

Table 3. Duration (years) of the age-state and ontogeny in some steppe grasses.

Species	Habitat	Age-States						Duration of full ontogeny
		j	im	v	g ₁	g ₂	g ₃ + ss	s
<i>Stipa pennata</i>	Dry steppes (Kustanai Region)	3	3	8	8	9	14 + 20	10
	Northern steppes* (Kursk Region)	1-4		2-3		20-25		10
<i>Festuca valesiaca</i> subsp. <i>sulcata</i>	Semidesert (Caspian Lowland)	1		2	5	10	6	5
	Northern steppes** (Kursk Region)	0.1-0.6		1-2	2-4	18-19	5-8	5
	Dry steppes (Kustanai Region)	2-3	3	5	2	6	11 + 8	4

*Data of Golubeva (1964).

**Data of Persikova (1959).

and more isolated. However, little rejuvenation occurs, the particles age and die off. Such vegetative propagation cannot ensure prolonged existence of the coenopopulation in the absence of reproduction of seeds.

Survival of age-states

The individuals of different age-states are characterised by uneven rates of annual survival which increase in the first part of ontogeny and reach 100% in the mature state. This mature period is associated with active shoot formation in the tussock and growth of the root system which may reach depths of 100–150 cm and diameters of 60–80 (up to 100) cm in *Stipa pennata* and *Festuca valesiaca*. The plants become weaker when they reach the senile state, a considerable number of shoots and roots die off and the survival rate is consequently reduced.

To characterise the death of coenopopulations of different steppe grass species depletion curves (Harper 1977) were drawn. They correspond to the negative exponential (Fig. 3A), indicating a relatively constant death rate; even an abrupt fluctuation of conditions (such as a drought in 1975) did not affect the depletion rate of plants. The half-life period was 20.5 years in *Stipa pennata* and 13.7 years in *Festuca beckeri*. In steppe firm-tussock grasses the decay of the coenopopulation is, as a rule, rather slow; this is due both to the stability of individuals and to the considerable duration of age-state ontogeny. Using the data on the death rate of plants of different age-states in *Stipa pennata* coenopopulations ($se = 90-97\%$; $pl = 84$, $j = 66$, $im = 40$, $v-g_2 = 0$, $g_3 = 26$, $ss = 76$, $s = 73$, on the basis of genet number) we attempted to plot a survival curve for one generation of seedlings ($pl = 100$) (Fig. 3B). Biological rather than chronological time (that is, using age-states) is plotted on the horizontal axis. As might be expected, the curve shape approximates type III of Deevey (Harper 1977). This however is not necessarily contradictory to the exponential type of depletion (Fig. 3A) curves. Survival seems to correspond frequently to the exponential *within* different age-stages during ontogeny, whereas the total survivorship curve may be represented as a combination of a few such curves, with different inclination angles, each of them corresponding to a certain age-stage. Sarukhán (1978) reached a similar conclusion.

The number of plants in coenopopulations of tussock grass species does not change greatly in time (Fig. 3C). The stability is related to scanty seed reproduction, adult plant stability and considerable life span of particles and whole clones.

Reproduction

In coenopopulations of tussock grasses inflorescences are not formed by all individuals having reproductive capacity. Intermittent flowering, reported for many plant species (Rabotnov 1978) is rather typical of the dense-tussock steppe grasses. The intervals are particularly long in old plants: some individuals form 1 or 2 generative shoots only once in 7 or

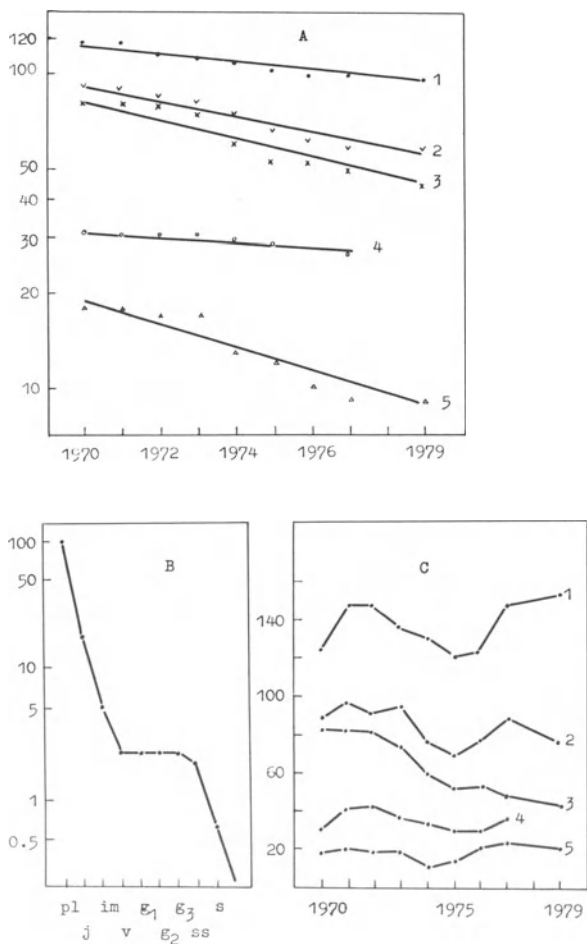


Fig. 3. Survival and dynamics of grass coenopopulations.

A. Depletion curves for coenopopulations: 1, *Stipa pennata*; 2, *Festuca beckeri*; 3, *Koeleria glauca*; 4, *Stipa capillata*; 5, *Koeleria macrantha*. The numbers of individuals on a $10 \times 0.5 \text{ m}^2$ transect from the population of 1970 are shown on the ordinate.

B. Calculated survival curve of *Stipa pennata* individuals during ontogeny; age-states are indicated on the abscissa and the number of surviving individuals on the ordinate.

C. Dynamics of plant numbers (system II calculation units) for 10 years on a $10 \times 0.5 \text{ m}^2$ transect: 1, *Stipa pennata*; 2, *Festuca beckeri*; 3, *Koeleria glauca*; 4, *Stipa capillata*; 5, *Koeleria macrantha*. The number of calculation units is shown on the ordinate.

8 years. The rise and fall of reproductive activity in different grass species may not coincide; for example, *Stipa pennata* and *Festuca beckeri* have different periods of inflorescence initiation and development. The particules of some grass species (*Festuca beckeri*, *Koeleria macrantha*, *K. glauca*, *Phleum phleoides*) retain the ability to flower almost until they die and can be observed in particules with 1–2 vegetative shoots. While the efficiency of such flowering is very low, there is still the possibility of seed formation. Furthermore, the presence of temporarily sterile individuals

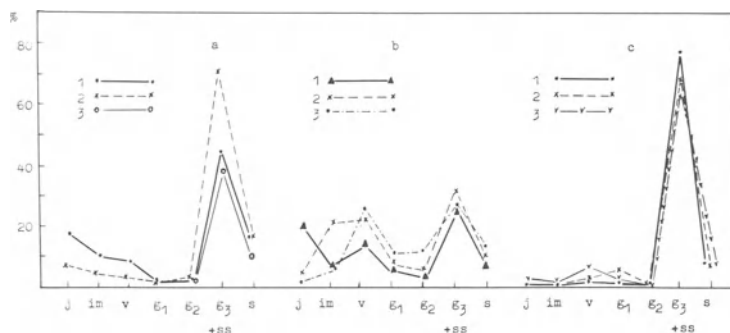


Fig. 4. Age-state spectra of coenopopulations of some grasses in sandy steppes on a preserve area (data of 1972). (a) *Stipa pennata*. The proportion of each age-state group in a coenopopulation (%) is shown on the ordinate: 1, % of total genet number; 2, % of the total number of individuals of seed and of vegetative origin (genets + ramets); 3, % of clones within genets. (b) *Stipa capillata* (1), *Festuca beckeri* (2), *Cleistogenes squarrosa* (3); (c) *Koeleria glauca* (1), *Koeleria macrantha* (2), *Phleum phleoides* (3). The proportions of each age-state group as a % of total genet number is shown for (b) and (c).

in a coenopopulation pre-empt space from occupation by other individuals and results in the maintenance of genetic diversity in the coenopopulation.

Age-state spectra

The age-state spectra of coenopopulations in many firm-tussock grasses growing in a particular community are rather similar (Fig. 4): the absolute maximum in the spectrum occurs in $g_3 + ss$ specimens, and the minimum in those of g_2 . Some years are characterised by local maxima in the group of young individuals. If system III calculation units are used (that is, including particules within clones) the predominance of old plants proves to be still more notable (Fig. 4a).

A review of age-state spectra (Fig. 5) of some firm-tussock grass species in different communities suggests that in some habitats a species is characterised by a particular relationship between plants of different age-states in the stable part of the population ($g_1 + g_2 + g_3 + ss + s$). *Festuca valesiaca* is, as a rule, characterised by total predominance of young individuals ($j + v + g_1$) over the old ones ($g_3 + ss + s$) or their more or less equal relationship. In *Stipa lessingiana* two types of spectra are distinguished — with maxima on g_2 in the stable part (Fig. 5BI) or on old individuals (Fig. 5BII). It should be noted that the maximum on old individuals of *Festuca valesiaca* subsp. *sulcata* and *Stipa lessingiana* is typical of non-grazed localities while the maximum on $g_1 - g_2$ is usually observed on continuously grazed plots. In *Stipa pennata*, the age-state spectrum in most of the habitats investigated is characterised by a predominance of old plants (Fig. 5C); the northern steppe (Kursk Region) is characterised by the predominance of reproductive plants (g_3) among the old ones and higher participation of mature plants (g_2); in the

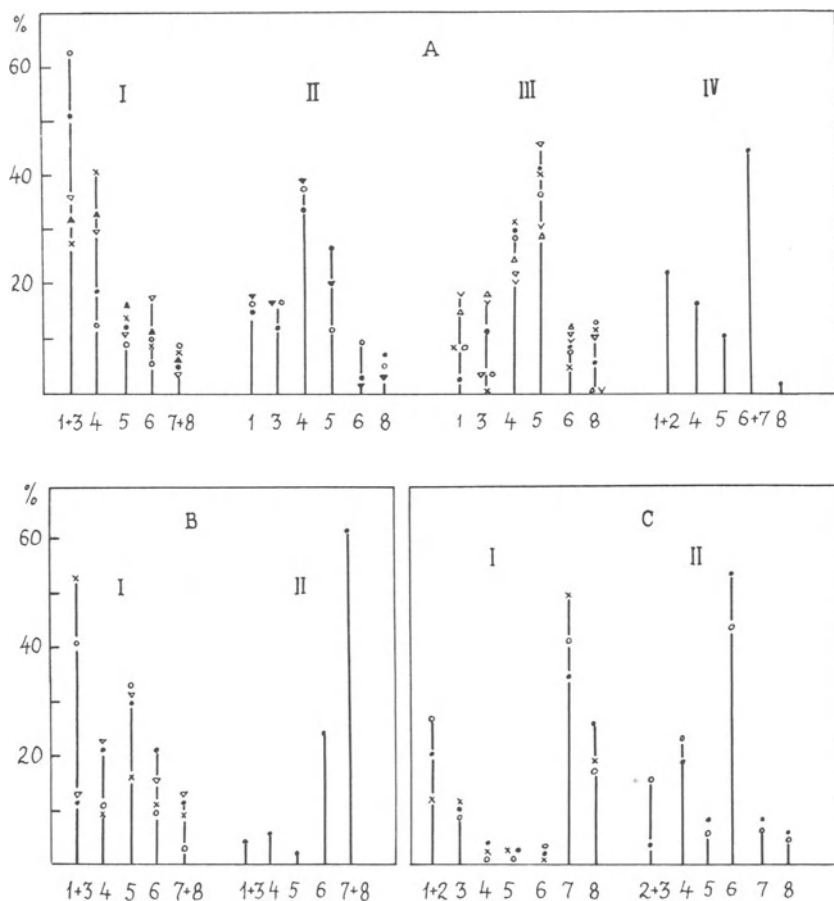


Fig. 5. The age-state spectra of coenopopulations of some firm tussock grasses. The proportions of various age-state groups in coenopopulations are shown on the ordinate. 1, j; 2, im; 3, v; 4, g₁; 5, g₂; 6, g₃; 7, ss; 8, s.

(A) *Festuca valesiaca* subsp. *sulcata* growing in (I) steppes of Central Kazakhstan (Borissova and Popova 1972), (II) semidesert of North Caspian area under low and moderate grazing (Vorontzova and Zhukova 1976), (III) arid steppes of Inland Tian-Shan (Kozhevnikova and Trulevich 1977) and microsinks in the semidesert of North Caspian area (Vorontzova and Zhukova 1976), (IV) arid steppes of Naurzum Preserve without grazing.

(B) *Stipa lessingiana* growing in (I) arid steppes of Central Kazakhstan (Borissova and Popova 1972), (II) arid steppes of Naurzum Preserve without grazing.

(C) *Stipa pennata* growing in (I) sandy steppes of Naurzum Preserve, (II) northern steppes of the European part of the USSR. Each symbol on the vertical lines corresponds to a particular coenopopulation.

sandy steppes (Kustanai Region) subsenile plants (ss) are predominant (Fig. 5CI).

The following indices were used to characterise the dynamic processes in grass coenopopulations (Table 4). (On permanent grass plots system III calculation units were used.)

1. Death rate of plants, determined as $f.100/N_1$, where f is the number of plants dying in the period between two successive observations and N_1 is the plant number at the first of the two observations.
2. The rate of coenopopulation growth $(\ln N_2 - \ln N_1)/(t_2 - t_1)$, where N_2 is the number of plants during the second of two successive observations.
3. The rate of ontogenetic change $q.100/N_1$, where q is the number of plants that changed their age-state between t_1 and t_2 .
4. Coenopopulation age-state index Δ (Uranov 1975), which estimates the coenopopulation age-state level on the basis of age-state group relationship: $\Delta = \Sigma k_i m_i / \Sigma k_i$, where k_i is the number in each age-state group and m_i is the age 'value' of one individual of the corresponding group. The values of m_i are calculated on the basis of the logistic curve and expressed as follows: $j = 0.018$; $im = 0.047$; $v = 0.119$; $g_1 = 0.270$, $g_2 = 0.500$, $g_3 = 0.731$; $ss = 0.880$; $s = 0.953$. This index Δ changes from 0 to 1 and increases with coenopopulation ageing; Δ for two successive time intervals is shown as a fraction in Table 4. The theoretical basis of this calculation is discussed by Uranov (1975).
5. The number of juvenile individuals of the first year of life.
6. The number of particles arising from previously existing plants, that is, the number of individuals that appeared vegetatively.

The dynamic processes in coenopopulations of dense-tussock grasses can be characterised as follows (Table 4):

1. The death rate of seed individuals and particles varied from year to year. The maximum indices do not always coincide with the most unfavourable years: for example, after the drought in 1975–1976 the death rate of *Festuca beckeri* was no higher than in the previous years.
2. The death rate increased during the middle of the observation period and fell again by the end of it.
3. The differences between such indices as the death rate of the initial coenopopulation (or depletion rate) and the death rate of the whole coenopopulation are related to the fact that in the second index the death of all newly formed individuals is taken into account, which causes fluctuations of this index from year to year.
4. The rate of coenopopulation growth was low; coenopopulation numbers increased mostly on account of particle formation. If seed recruitment to the coenopopulation is considered alone, the growth rate becomes negative.
5. The ontogenetic development was uneven. Considerable changes in age-state composition occurred in the years after drought (1976–1977), when the plants were subjected to intensive ageing, resulting from the death of a great number of shoots in tussocks.
6. The recruitment of seed progeny was uneven.
7. The coenopopulations of *Festuca beckeri* revealed a somewhat higher death rate than those of *Stipa pennata*.
8. The rate of coenopopulation growth (assessed by number of genets)

Table 4. Parameters of grass coenopopulation dynamics on a permanent transect ($0.5 \times 10 \text{ m}^2$) in Naurzum Preserve. Seedlings are excluded.

Species	Parameters	Observation periods									
		1970– 1971	1971– 1972	1972– 1973	1973– 1974	1974– 1975	1975– 1976	1976– 1977	1970– 1977		
<i>Stipa pennata</i>	1. Death rate (%)	2.4	4.7	6.0	9.5	9.1	11.5	3.2	30.5		
	2. Coenopopulation growth rate in the first year of life	+0.17	0	–0.08	–0.4	–0.07	+0.02	+0.18	+0.17		
	3. Rate of ontogenetic change	2.0	3.3	8.0	8.3	7.4	9.7	9.4	7.6		
	4. Age-state index (Δ)	0.70	0.58	0.57	0.60	0.63	0.66	0.75	0.70		
		0.58	0.57	0.60	0.63	0.66	0.75	0.76	0.76		
	5. Number of juvenile individuals in the first year of life	25	6	0	0	2	1	1	35		
<i>Festuca beckeri</i>	6. Number of separated particles	0	1	0	7	1	15	26	50		
	1. Death rate (%)	1.1	6.2	5.5	12.6	10.4	8.6	7.8	33.6		
	2. Coenopopulation growth rate in the first year of life	+0.07	–0.06	–0.05	–0.12	–0.09	+0.09	+0.15	0		
	3. Rate of ontogenetic change	6.7	8.2	15.4	11.5	16.9	15.7	24.7	14.1		
	4. Age-state index (Δ)	0.59	0.57	0.58	0.60	0.63	0.66	0.73	0.59		
		0.57	0.58	0.60	0.63	0.66	0.73	0.82	0.82		
	5. Number of juvenile individuals in the first year of life	8	0	0	1	1	0	0	10		
	6. Number of separated particles	0	1	0	0	13	24	0	38		

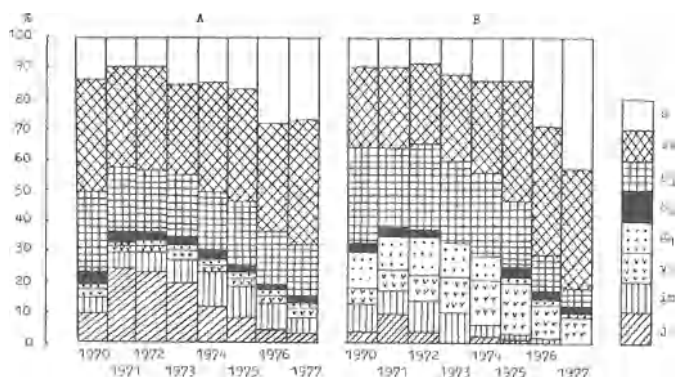


Fig. 6. Changes of some age-state spectra of coenopopulations of *Stipa pennata* (A) and *Festuca beckeri* (B). The proportions of age-state groups (% of the total number of individuals) are shown on the ordinate.

was higher in *Stipa pennata* than in *Festuca beckeri*; this reflects the more plentiful regeneration in *Stipa*.

9. The ontogenetic changes are more variable and evident in *Festuca beckeri* than in *Stipa pennata*.

The basic processes occurring in the course of time in the coenopopulation (the appearance of new individuals, their ontogenetic development, and the death rate which is specific for different age-state groups) determine the dynamics of coenopopulation age spectra. Although the main characteristics of the spectra during eight years of observations were retained in the grasses, some changes in age-state group relationships did occur (Fig. 6). The share of *j* and *im* became reduced to zero in *Festuca beckeri*. The relationships in the young part of the coenopopulation underwent wave-like changes caused by death and ontogenetic development of individuals. The share of *ss* individuals and *s* age-states increased, particularly after the drought of 1975. The consequences of drought were manifested in a reduced number of vegetative and reproductive shoots in 1975, by increased formation of particules and by particule ageing. Thus, the changes in age-state spectrum are related to the population characteristics of species and the effect of the environmental variations through time. In 1979 many seedlings (22) and juvenile individuals (17) of *Stipa pennata* were recorded on the transect, suggesting that grass coenopopulations are replenished periodically by small portions of new seed individuals, roughly after 9–10 years.

In coenopopulations of the grasses investigated the permanent individuals (that is, those retained during the whole observation period) make up not less than 50 percent of all recorded individuals: the flow of deaths and regenerations is stabilised by the permanent part of the coenopopulation. We tried to estimate these relationships quantitatively using a parameter which we call 'balance lability', calculated as $1 - (N'/N)$, where N' is the number of plants permanently retained during the whole

observation period and N is total number of recorded plants (using system III calculation units). The index can be used to estimate the degree of population flux. The higher the balance lability, the more dynamic the coenopopulation. In steppe grasses the index is equal to about 0.53.

Phytomass and phenology

While the numbers and age-state composition of grass coenopopulations are characterised by relative stability, the phytomass is a more dynamic index and can change annually (Gordeyeva 1976). This is due primarily to changes in the degree of shoot formation in tussock grasses. From our observations some particules do not form shoots at all in dry years, that is, they are in a state of secondary dormancy. This characteristic is particularly abruptly manifested in grasses under very adverse conditions for growth, where the period of dormancy may last up to 3 years (Steshenko 1976, Borissova et al. 1976).

One of the essential aspects of the population biology of a species is its development rhythm throughout the year, or phenology. Most species of steppe grasses form a rather integral group with regard to the rhythm of seasonal development. The leaves start growing in April–May, reach maximum development in mid-June, while at the end of June–July the leaf tips begin to dry. In years of drought leaves start to dry earlier and more rapidly; even in less extreme years up to 80% of total leaf area may dry out by the end of the summer. The grasses can survive the warmest and driest period of the summer in a state of temporary dormancy. New leaves appear in autumn and remain green under snow. The reproductive shoots of *Stipa pennata* are initiated in autumn, those of other species are established in spring prior to flowering (*Festuca*, *Koeleria* and others). The species of *Stipa* usually flower in the middle and at the end of May, those of *Festuca* and *Koeleria* at the beginning of June. In some species (*Stipa capillata*, *Cleistogenes squarrosa*) flowering is delayed until mid-summer.

Physiological characteristics

The considerable similarity of the population biology of steppe grasses is based on their common ecological characteristics. The narrow-leaved steppe grasses were classified by Kolpikov (1960) in an ecological group which he named 'stipaxerophytes'. Their ecological and physiological characteristics explain to a considerable extent the stability of steppe grasses in arid conditions. These species are characterised by a high threshold of protoplasm coagulation (55–63°C); low water content (down to 38% of plant fresh weight, Grigoryev and Razumova 1974) 79% of which is bound water (Zhuravleva 1977), retained after water extraction by a 30% glucose solution; high protoplasm viscosity and relatively high (maximum up to 35–40 atm) osmotic pressure (Sveshnikova and Bobrovskaya 1973); the latter determines the considerable root suction in steppe grasses. The stipaxerophytes have relatively low transpiration rates (usually less than $1.5 \text{ g.g}^{-1} \text{ hr}^{-1}$) particularly in the drought period

(Gorshkova and Kopytova 1977), enabling them to resist dehydration. Because of their low content of free water the stipaxerophytes have a relatively low photosynthetic rate (Spivak 1977). The rate and regulation mechanisms of water balance determine the distribution of grasses in nature and their role in coenoses (Sveshnikova 1979). *Stipa sareptana* dominates in the most xeromorphic conditions of desert steppes. Its water balance is regulated by variations of water regime indices (transpiration rate, water content in leaves, osmotic pressure), by the rhythm of stomatal functioning and by rolling and unrolling of leaf blades. *Stipa rubens* and *S. pennata* are characterised by higher transpiration rates, lower variability of water regime indices, and by absence of leaf rolling: these species are typical of more northern steppes. In the south of the steppe zone they occur either on light-textured soils or under high moisture conditions. *Festuca valesiaca* subsp. *sulcata* has a very plastic water balance that permits it to survive in a wide range of conditions (Sveshnikova 1979).

Grazing

The steppe tussock grasses make up the basis of climax communities and are subject to intensive grazing. While in the pre-agricultural period the grazing of wild animals in natural conditions was necessary for equilibrium maintenance (Semenova-Tyan-Shanskaya 1978), with modern agricultural management the development of many steppe plants is influenced by intensive grazing. The effect of grazing, however, is versatile and not unequivocal. With steppe grasses grazing affects the vitality and numbers of plants in coenopopulations and their age-state spectrum (Zaugolnova 1977). The response of species to grazing is to a great extent specific and depends on grazing intensity. Thus in some species (*Festuca valesiaca* subsp. *sulcata*, *F. beckeri*) the first stages of grazing can be associated with improved vitality of individuals and clones, an increase in the number of vegetative and reproductive shoots and their height. The basic reason for such behaviour lies evidently in the attenuation of the dominant *Stipa* species that are strong competitors. With increased grazing the vitality of the *Festuca* spp. is worsened. In *Stipa caucasia* and *Agropyron pectiniforme* even slight grazing is associated with a decrease in tussock diameter, as well as shoot number and height (Kozhevnikova and Trulevich 1971).

Intensive grazing affects not only plant vigour and number but also leads to rearrangement of the age-state spectrum (Kozhevnikova and Trulevich 1971): the number of old plants is reduced because of their high death rate; there is also a 'false rejuvenation' of coenopopulations, related to the accumulation of young plants, the impossibility of complete ontogeny and the death of plants that have not reached the natural limits of life.

Conclusion

The above review makes it possible to distinguish the most common coenopopulation characteristics of steppe tussock grasses.

1. The formation of compact tussocks with strong root systems leads to high survival of adult individuals;
2. The considerable length of tussock life allows old individuals to accumulate in a coenopopulation;
3. The numbers and age-state composition of coenopopulations are stable;
4. Both the numbers of reproductive shoots and the vegetative mass are dynamic.

These characteristics determine the dominating and edificator role of tussock grasses. Even grass species with low abundance in steppes are extremely stable components, retaining their positions in the coenosis for a long time.

Short-rhizome herbs

In sandy steppes this group is represented by *Potentilla cinerea*, *Centaurea sibirica*, *Arenaria procera*, *Hieracium echinoides*, *H. virosum*. Our observations of *Potentilla cinerea* and *Centaurea sibirica* may be used to exemplify the group. While each species has its own specific characteristics of coenopopulation growth and dynamics, they are all similar in many points.

The potential seed yield in these species is rather different (Table 5); the actual yield is similar. The latter index varies slightly over time, whereas the potential yield may vary rather strongly. The fluctuations in potential yield are related primarily to the number of reproductive shoots formed on a plant. The reproductive organs are initiated in these species in the previous summer, and the drought occurring in this period may have a negative effect on the number of reproductive shoots (as for example in 1976, see Table 5). These two species flower at the end of May, and are insect pollinated. It is possible that with a small number of reproductive shoots and flowers pollination may be more efficient. Many seeds of *Potentilla* and *Centaurea* are damaged by weevil larvae. If flowering is poor, the number of phytophagous insects may drop abruptly and the seed damage is reduced in these years.

Table 5. Seed yield and its components (per 1 m²) in short-rhizome plants on Naurzum Preserve.

Species	Year	Number of reproductive shoots	Number of flowers (inflorescences)	Potential yield	Actual yield
<i>Potentilla cinerea</i>	1973	27.2	61.8	1876.8	64.7
	1974	14.6	34.6	1051.2	49.8
	1976	3.4	9.3	275.4	58.7
<i>Centaurea sibirica</i>	1974	6.9	161.4(6.9)	161.4	56.3
	1977	11.0	249.0(11)	249.0	75.8

The seeds of *Potentilla cinerea* usually germinate in close proximity to maternal plants, giving rise to groups of 20–40 seedlings. The fruits of

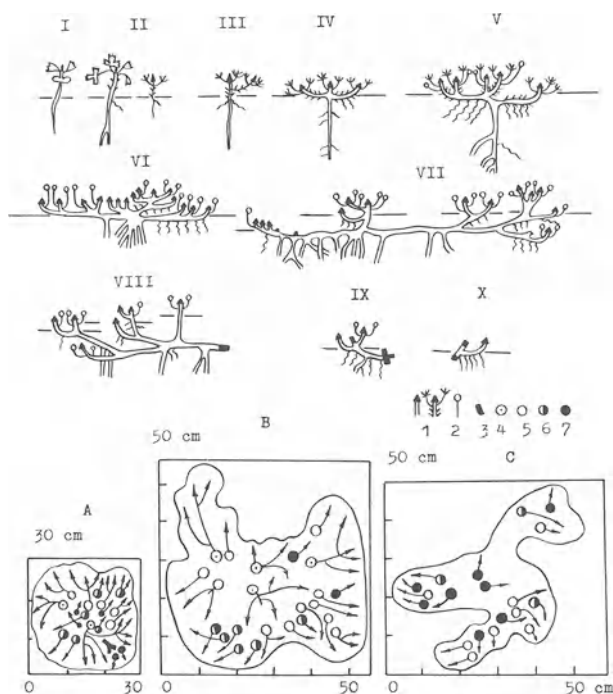


Fig. 7. Age-states and clone structure in *Potentilla cinerea*. The individuals of seed origin are shown as: I, seedling; II, juvenile; III, immature; IV, virginile; V, young; and VI, mature reproductive. Individuals of vegetative origin are: VII, mature; VIII, old strong; IX, old weak; X, senile. 1, vegetative shoot; 2, reproductive shoot; 3, dead shoot. Individuals of vegetative origin are: 4, mature; 5, old strong; 6, old weak; 7, senile. A, B, C, the stages of clone development.

Centaurea sibirica may be carried away by beetles picking the fleshy tendrils; the seedlings of this species are, as a rule, randomly distributed. The number of seedlings of *Potentilla cinerea* is rather high in some years; *Centaurea sibirica* seedlings are always sporadic. However the survival of small *Potentilla* seedlings is rather low, and by the end of summer fewer than 1–2 per 5 m² persist. Seedling density of *Centaurea sibirica* by the end of summer is the same.

The coenopopulations are replenished extremely slowly: during the whole observation period (1970–1979) on a transect (0.5 × 10 m²) only one juvenile individual of *P. cinerea* became established but not a single one of *C. sibirica*. These species are characterised by clone formation in mature and old age-states (Fig. 7) and the clones spread rather slowly. Some particles do not undergo rejuvenation and age gradually. When they die the vacant site is taken by the same or by other species. The dimensions of clones and the number of particles in each are different in these species: clone diameter in *P. cinerea* is 20–70 cm, in *C. sibirica* 10–20 cm; the average particle number per clones is 8.1–13.2 and 3.2–3.5 respectively. The differences affect the position of the species in a coenosis:

as a rule, the cover of *P. cinerea* is higher than that of *C. sibirica*. The clones of these species exist for a rather long period of time. An estimate of their life-span can be indirectly obtained by determining the particles' 'provisory age' (Gatsuk et al. 1980): the life-span of a *Potentilla* clone is not less than 50 years.

Coenopopulations of these species are composed of (a) individuals of seed origin, (b) clones consisting of particles (that is, individuals of vegetative origin) and (c) single particles, being the last fragments of clones. Together these give the total genet number. In short-rhizome plants different patches of a coenopopulation have different genet numbers, caused by differences in seed regeneration and in the death rates of isolated particles and of particles within clones. The number of ramets in a coenopopulation reflects the intensity of individual disintegration and the average ramet number in a clone; the latter varies from species to species. The numbers of genets and ramets for different coenopopulations of *Potentilla cinerea* and *Centaurea sibirica* are given in Table 6. The number of genets of *P. cinerea* varies within a small range and is only slightly reduced by grazing, whereas ramet number falls rather significantly. Haymaking and grazing cause the numbers to change within the same ranges as may be found on different coenosis patches on the Naurzum Preserve. For *P. cinerea* coenopopulations no serious effect of haymaking and grazing on the number of genets can be established but the number of ramets is higher on hay-fields and pastures, that is, there are more particles in the clone (on average) than on a preserve plot (without mowing or grazing). The coenopopulations of these species are characterised by the prevalence of old ($g_3 + ss + s$) particles (Fig. 8); the role of old particles is even higher in spectra calculated on the basis of ramet number. Seed regeneration is not abundant but it ensures the permanent presence of young individuals in the coenopopulation. This spectrum is rather stable and can last for a long period of time. The number of juvenile individuals can change both in time and space.

It is practically impossible to investigate the dynamics of individuals in short-rhizome species since their boundaries cannot be established without excavation. Thus in observations on permanent plots only the number of shoots was estimated. The numbers of vegetative shoots in *P. cinerea* and *C. sibirica* varied slightly during 8 years of observations: 334–380 in *P. cinerea* and 75–93 in *C. sibirica* on a $0.5 \times 10 \text{ m}^2$ transect, indicating coenopopulation stability. These plants are characterised by well-branched, deep (160–200 cm), adventitious and fleshy roots with water reserves in them. The compound leaves of *P. cinerea* are rather hairy and leaflets can fold along the midrib when air and soil dryness increase. These features of plant texture contribute to an increase in stability of the coenopopulations in arid conditions. *P. cinerea* and *C. sibirica* are typical of psammophytic and petrophytic variants of steppes, occurring in pine forests on sandy soils, as well as in the steppe and forest-steppe zone of the European part of the USSR, Kazakhstan and Siberia. They are scarcely eaten by cattle and withstand grazing. The vitality of individuals improves in the first stages of pasture deterioration and with heavy overgrazing,

Table 6. The composition of coenopopulations of some short-rhizome plants in different coenoses, based on 100 plots, each 0.5 m²

Species	Coenosis	Year	Individuals of seed origin	Clones	Particule number in clones	Number of single particules	Genets	Ramets (or particules)
<i>Potentilla cinerea</i>	Preserve	1971	221	34	348	—	255	348
	Preserve	1972	165	141	1374	—	306	1374
	Hayfield	1972	131	95	812	—	226	812
	Pasture	1972	118	85	571	—	203	571
<i>Centaurea sibirica</i>	Preserve	1971	54	101	357	173	328	530
	Preserve	1972	32	71	242	34	137	276
	Hayfield	1972	51	144	593	66	261	659
	Pasture	1972	80	197	789	37	314	826

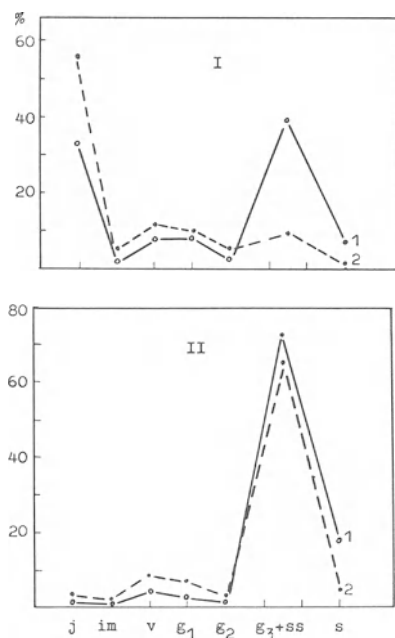


Fig. 8. Age-state spectra of short-rhizome plants: *Potentilla cinerea* (I) and *Centaurea sibirica* (II). The proportions of each age-state in a coenopopulation are shown on the ordinate; these are calculated either on the basis of total number of individuals (1) or on the basis of genet number (2). Data are shown for 1972.

when many species are eliminated from the grass stand, *P. cinerea* becomes the dominant of the coenosis. Their projective cover is not high (2–5%, maximum 12–15%), and because of their small height (5–7 cm) their occupation of space is 2–5 times lower than dense-tussock grasses. The foregoing population characteristics make them permanent components of sandy steppes.

TYPE II – TAP-ROOTED PERENNIAL PLANTS WITH SEED REGENERATION

This group is represented by species which regenerate in the climax community only by seed: *Artemisia campestris* (f.*sericea* and f.*glabra*; data reported here refer only to f.*sericea*), *Euphorbia seguieriana*, *Onosma simplicissimum*, *Gypsophila paniculata*. Root suckers can potentially be formed in *Euphorbia seguieriana* but is not observed in the climax community of sandy steppes. Vegetative propagation is also absent in these plants in the old age-state. The potential seed productivity varies in mature individuals of these species within a wide range: it is highest in *Artemisia campestris* (4,200–12,700 ovules per individual) and the lowest in *Euphorbia seguieriana* (24–95). Numerous seedlings are formed in favourable

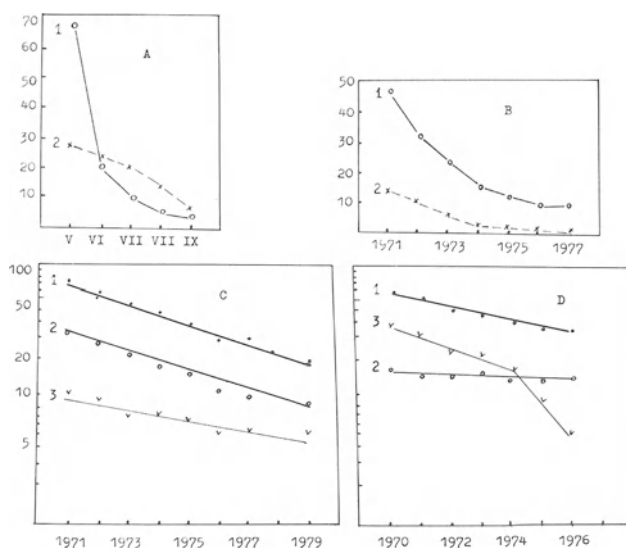


Fig. 9. Survival of tap-rooted plants in coenopopulations.

(A) Survival of seedlings during the vegetation period (May–September) on Naurzum Preserve in 1971: 1, *Artemisia campestris*; 2, *Euphorbia seguieriana*. The number of seedlings on a $10 \times 0.2 \text{ m}^2$ transect is shown on the ordinate.

(B) Survival of juvenile individuals recorded in 1971, from 1971 to 1977. The number of individuals on a $10 \times 0.5 \text{ m}^2$ transect is shown on the ordinate. 1, *Artemisia campestris*; 2, *Euphorbia seguieriana*.

(C) Depletion curves for all individuals recorded in 1971 on a $10 \times 0.5 \text{ m}^2$ transect. 1, *Artemisia campestris*; 2, *Euphorbia seguieriana*; 3, *Onosma simplicissimum*.

(D) Depletion curves of: 1, *Scorzonera ensifolia*; 2, *Seseli ledebouri*; 3, *Helichrysum arenarium*.

years but most of them die off in the course of summer (Fig. 9A); the survival of seedlings is related to seed size and this is higher in *E. seguieriana*. Juvenile plants may be numerous in the population but the death rate is so high (Fig. 9B) that their participation in the coenopopulation decreases abruptly in the first few years after their appearance. Thus seed regeneration in these species is sporadic. The share of juvenile individuals recorded in the coenopopulation is higher (on average 40–50%) than in the groups of species discussed previously.

The underground part of these plants become branched with ontogenetic development and the root system reaches a depth of 160–200 cm in the mature state. In the first stages of ontogeny the stability of individuals in coenoses increases somewhat and their death rate decreases correspondingly. As plants age their shoots die and the tap root deteriorates, the depth of root penetration is reduced and plant stability declines. Plant survival changes correspondingly during ontogeny. For example in *Artemisia campestris* the % survival of each age-state changes in the following way: j – 27, im – 44, v and g₁ – 72; g₂ – 100; g₃ and ss – 65; s – 70. One of the essential differences between this type of population

behaviour and that of bunch or tussock plants is the lower survival at the beginning and the end of the ontogeny of the tap-rooted plants. In spite of the higher number of juvenile individuals at some periods in a coenopopulation the total number (per 0.5 m²) is not high in these species: 0.1–7.3 individuals in *Artemisia campestris*, 0.5–0.8 in *Onosma simplicissimum* and 0.2–3.1 in *Euphorbia seguieriana*.

The species investigated in the sandy steppes are characterised by a rather long life span of the pre-reproductive period (Table 7), one of the reasons for an accumulation of this age-state. The ageing period ($g_3 + ss + s$) is somewhat extended. The total life span is, on the whole, shorter than in tussock plants of Type I.

The coenopopulation number varies considerably in time. In coenopopulation of *Artemisia campestris* an increase in number was recorded only once in nine years of observations, and twice in coenopopulations of *Onosma simplicissimum* and *Euphorbia seguieriana*. The rises are related to the sporadic formation and rooting of seedlings. The depletion rate of individuals in a coenopopulation (Fig. 9C) scarcely changes in different years and seems to depend little on environmental fluctuations. The depletion curves are in all cases close to the exponential relationship and the species differ slightly in death rate. The population half-life is shortest in *A. campestris* (4.0 years), 4.7 years in *E. seguieriana* and 5.0 years in *O. simplicissimum*.

The comparison with tussock plants reveals another essential characteristic of the population behaviour of tap-rooted plants: their number is much more dynamic, suggesting that they are relatively labile species: balance lability is 0.81–0.87 in *A. campestris* and *E. seguieriana* and 0.69 in *O. simplicissimum*.

Although the depletion rates (of plants present from the first observation) do not change in time (Fig. 9) the death rate sometimes increases greatly (Table 8). This was caused mainly by death of young plants that appeared in 1971. The growth rate of a coenopopulation varies from year to year, but negative indices prevail over positive ones: the coenopopulation number decreases significantly during the nine-year period.

The age-state spectra of coenopopulations of the tap rooted species are characterised by the following features (Fig. 10): the absolute maximum occurs as a rule among the individuals of the pre-reproductive period, or of g_1 ; the position of the maximum is mobile and depends on the rate of initial development of individuals, their death rate and on the sporadic appearance of seedlings; the height of the maximum in the spectrum depends on the intensity of species seed reproduction and on the time that has passed since mass seedling appearance; local maxima may appear among the old individuals, caused by a slightly extended ageing period; the longer the plant ontogeny the more important and stable is the maximum on g_3 (Table 7, Fig. 10).

The characteristics of ontogenetic development account for another essential aspect of population behaviour of this group of species, namely the dynamism of the age-state spectra in time, as may be illustrated by *Artemisia campestris*. During the whole observation period (Fig. 11) the

Table 7. The duration of age-states and ontogeny (years) in some tap-rooted species on permanent plots in the Naurzum Preserve

Species	Duration of age states							Total duration of the ontogeny	
								Ranges	Average
	j	im	v	g ₁	g ₂	g ₃	ss		
<i>Artemisia campestris</i>	3-7	1-5	2-6	1-5	2-4	2-8	1-3	14-42	30
<i>Euphorbia seguieriana</i>	1	5-8	-	4-7	2-5	2-6	1-2	15-29	20
<i>Otosma simplicissimum</i>	4	4	5	10	6	3	not ascertained		about 40

Table 8. Some indices of dynamics of *Artemisia campestris* coenopopulations on a $0.5 \times 10 \text{ m}^2$ transect in the Naurzum Preserve. Seedlings are omitted.

Parameters	1970-1971	1971-1972	1972-1973	1973-1974	1974-1975	1975-1976	1976-1977	1970-1977
Death rate (%)	1.2	21.1	16.9	19.7	23.5	23.1	0	67.3
Growth rate of coenopopulations	+0.12	-0.41	-0.34	-0.92	-0.69	-0.51	0	-1.1
Degree of ontogenetic change (%)	9.4	3.3	16.9	27.9	13.7	23.1	30.0	68.4
Age-state index	$\frac{0.20}{0.19}$	$\frac{0.19}{0.22}$	$\frac{0.22}{0.25}$	$\frac{0.25}{0.31}$	$\frac{0.31}{0.35}$	$\frac{0.35}{0.40}$	$\frac{0.40}{0.45}$	$\frac{0.20}{0.45}$

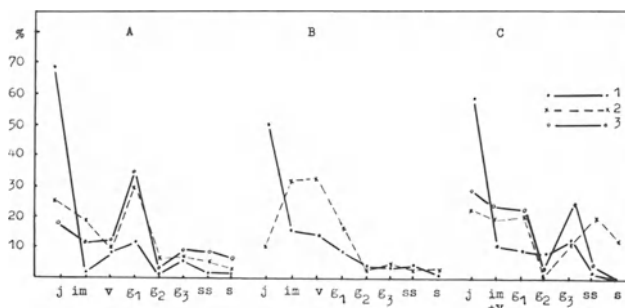


Fig. 10. Age-state spectra of coenopopulations of tap-rooted plants. The proportion (%) of the total genet number is shown on the ordinate. A, *Artemisia campestris*; B, *Euphorbia seguieriana*; C, *Onosma simplicissimum*. 1 and 2, Preserve area in 1971 and 1972; 3, hayland in 1972.

participation of juvenile individuals decreased abruptly while old ones increased. The share of *im*, *v*, *g₁* individuals is marked by wave-like changes: the absolute maximum moves from *j* to *g₁*. These changes are a result of the death of individuals and their age development. We did not succeed in establishing any relationship between fluctuations in meteorological conditions and the degree of ontogenetic changes: such changes seem to depend largely on population properties of the species. On the whole, the rate of ontogenetic change is much higher in this species than in dense-tussock grasses (compare Table 4), and is related to the shorter life-span of *Artemisia campestris* individuals.

The abundance of tap-rooted species increases with coenosis disturbance. *Artemisia campestris* f. *sericea* becomes dominant in a pine forest on disturbed sandy soils; *A. campestris* f. *glabra* reaches high numbers in the first stages of old field disturbance (up to 3–8 specimens per 1 m²), but in

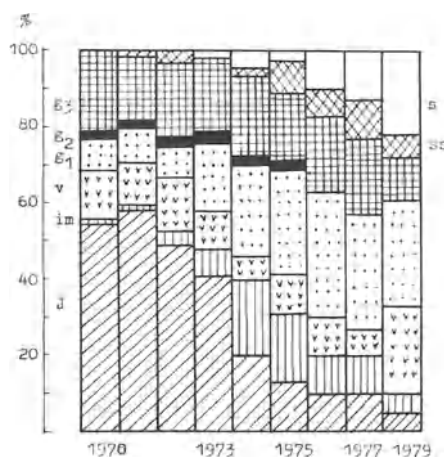


Fig. 11. Changes of the age-state spectrum of *Artemisia campestris* coenopopulation over nine years. The proportions of age-state groups (% of total number) are shown on the ordinate.

the natural community the density decreases abruptly (0.8–0.1). The numbers of *Euphorbia sequieriana* are increased by grazing 2.5–7 times, compared to the maximum number on a preserved area. The attenuation of interspecific plant interference results in their improved vegetative and reproductive growth, increased seed productivity and a correspondingly higher rate of coenopopulation growth.

The following are the most typical features of the population behaviour of these species: (1) the absence of vegetative propagation; (2) relatively high elimination of individuals; (3) a shorter ontogeny than that of tussock plants and reduced duration of the senile state; (4) greater dynamism of numbers and of age-state spectra.

TYPE III – TAP-ROOTED PERENNIALS WITH MIXED REGENERATION

This group is represented by the following species in steppe communities: *Scorzonera ensifolia*, *Seseli ledebouri*, *Helichrysum arenarium*. The potential seed productivity of species is extremely different: in *S. ensifolia* it is 20–40 ovules per specimen and in *S. ledebouri* 1000–3000 (rarely up to 6500) ovules per specimen. The actual seed productivity is very low in *S. ensifolia* (0.2–2.3% of the potential) and considerably higher in *S. ledebouri* (30–40%, though in some years it is 0.2–1.2%). The number of seedlings however is very low even in *S. ledebouri*: in favourable years, 2–4 per 10 m². Seedlings of *S. ensifolia* and *H. arenarium* are sparse.

Vegetative propagation was also recorded in these species. Buds on roots give rise to shoots which then form their own root system and can exist independently. According to their age-state, these plants may then be equated with juvenile or with immature plants. In some species the connection between the root-suckers and the maternal plant may last for a long time (*S. ledebouri*), while in others it is disturbed rapidly as a result of root rot or breakage. Individuals of vegetative origin may retain traces of their former connection with the maternal plant for a long time and in coenopopulation analysis such plants can be estimated separately. Plants originating from root suckers undergo age changes and therefore different age groups can be distinguished among them, similar to those derived from seed. The ratio between the individuals of seed and vegetative origin in a population varies in different plant species: the percentage vegetative progeny among the total number of individuals is 28–35% in *S. ledebouri*, 88–97% in *H. arenarium* and 99–100% in *S. ensifolia*. The vigour of vegetative propagation in these species is different and this accounts for observed variations in numbers of the species: the average number of individuals per 0.5 m² is 0.2–19.3 in *Helichrysum arenarium*, 0.4–1.3 in *Seseli ledebouri*, 1.4–6.1 in *Scorzonera ensifolia* (Naurzum sand steppe). In coenopopulations pre-reproductive plants are as a rule predominant. Consequently the population number of these species is rather variable in time; balance lability is 0.8–0.9. Their half-life is rather short: 3.3–2.5 years in *H. arenarium* and 7.0 in *S. ensifolia*. *S. ledebouri* is different and

coenopopulations of this species are more stable in time, with a balance lability of 0.56 and half-life of 20.5 years. The root suckers of this species are more viable and have a slower rate of development than the two other species.

The calendar ages of these species are difficult to determine. Observations on permanent plots and morphological analyses have shown that the life-span of individuals in sandy steppes is roughly 18–20 years in *Helichrysum arenarium*, 15–25 years in *Scorzonera ensifolia*, 20–30 years in *Seseli ledebouri*.

Root suckers are formed actively in humid years. Newly formed individuals die off in a manner similar to those derived from seed (Fig. 9D), showing an exponential relationship that does not reveal any dependence on environmental fluctuations and plant age (*H. arenarium* is an exception). A higher death rate in populations of these species does not result from active formation of vegetative propagules. For example in *Scorzonera ensifolia* (growing on a $0.5 \times 10 \text{ m}^2$ transect) the highest number of dead plants was recorded in 1977–1979, but only two out of 19 were young (age 2–3 years), the rest being perennial individuals; out of 11 plants that died off in 1972–1973 five were 1–2 years old, the rest were older. The death of vegetatively formed individuals seems to be primarily an endogenous process in this species, determined by the survival level of individuals and the duration of their ontogeny. The survival of vegetative progeny may possibly depend on attachment to the maternal plant: the half-life is considerably greater in species where the connection is retained for a longer period of time.

Plants of the species investigated have different means of survival in arid conditions: in *Scorzonera ensifolia* the leaf bases are densely covered with long hairs which coat the young growing parts like a blanket; in *Helichrysum arenarium* both leaves and stems are hair-covered; in *Seseli ledebouri* the finely dissected leaves are covered with cuticula. The thick and succulent roots of *S. ledebouri* and *Scorzonera ensifolia* have water reserves in them that enables them to tolerate drought periods. Vegetative propagation of these species is intensified in areas where the plant cover is damaged by digging animals. Souseliks and blind rat-moles often eat the sappy roots of *S. ensifolia*, thus activating vegetative propagation: the density of this species may rise abruptly in such sites. However, these tap-rooted species are sensitive to grazing and are rapidly eliminated from the community by it.

The population behaviour of this species group reveals a considerable similarity with the previous group of species: the coenopopulations are, as a rule, characterised by a rather high lability of number and age-state composition, sporadic regeneration and predominance of young plants. The main difference lies in their dependence on vegetative propagation rather than seed reproduction. Vegetative progeny are more viable than seed progeny, and the death rates of juvenile and adult plants do not differ as sharply as in species with seed regeneration.

The tap-rooted plants with mixed self-maintenance may be considered as the relatively labile fillers of communities, rapidly colonizing disturbed areas and retaining their place for varying periods of time.

TYPE IV – TAP-ROOTED PLANTS WITH A SHORT ONTOGENY

In the steppes, this type is exemplified by *Alyssum lenense*, *A. tortuosum*, *Syrenia sessiliflora*. The density of these species on undisturbed plots of a community is usually low (approximately 0.4–1.4 specimens per 1 m²) but it can grow abruptly after disturbance, reaching an average of 20 specimens per 1 m². The life-span of plants is short, reaching 2–3 years in *Syrenia sessiliflora* and under 7–9 years in *Alyssum lenense*. The senile period is not pronounced in plant ontogeny. Most individuals in populations of *Syrenia sessiliflora* are monocarpic, with only some of them flowering for a second time or vegetating one more year after flowering.

These species are marked by a high death rate of individuals: 95.4% of the initial coenopopulation of *A. lenense* died in the period 1970–1979. This is caused primarily by the thin and shallow root system which only reaches a depth of 50 cm. Coenopopulations of these species decrease catastrophically after droughts. Coenopopulation numbers and age-state spectra are rather dynamic (Fig. 12) and subject to abrupt variations in time and space (Zaugolnova 1976). Young plants are predominant. Coenopopulation lability is due to the following factors: periodicity in

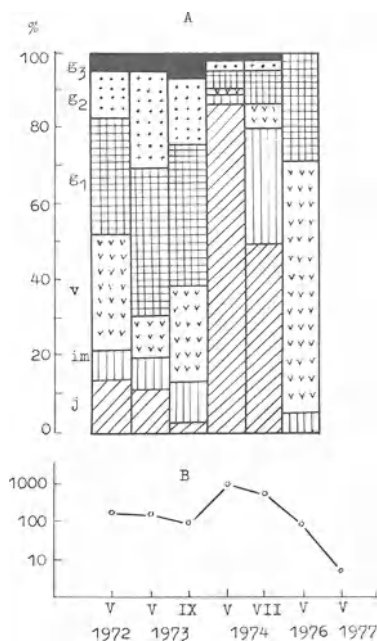


Fig. 12. Changes of the age-state spectra and the numbers of *Alyssum lenense* coenopopulations over time.

(A) Age-state spectra, showing the proportions of different age-state groups (% of the total number on a 15 × 0.5 m² transect); years and months of observations are shown on the abscissa.

(B) Changes in the total number of individuals on the same transect.

seedling establishment (the number of seedlings per 1 m² varies from 1 to 70 annually), high death rate of individuals, and rapid ontogenetic development. The balance lability of *Alyssum lenense* is about 1, that is, during the observation period (1970–1979) almost all individuals in the coenopopulation were replaced by others. The coenopopulation half-life in *A. lenense* varies from 1.2 to 2.7 years depending on the environment: death in these species is distinctly related to environmental fluctuations.

The species of this group are highly dynamic and marked by low competitive capacity. They are close in behaviour to exlerent species (Ramenskii 1938): they can rapidly occupy disturbed areas but are rapidly suppressed by other species as well.

TYPE V – LONG-RHIZOME PERENNIALS

In the sandy steppes this group is represented by *Carex supina*, *Veronica spuria* and *Galium ruthenicum*. Coenopopulation maintenance is basically by vegetative propagation and the species occur permanently in steppe communities on sandy soils, although their cover is not large. The ratio between progeny derived from seed and vegetative propagules varies: *Carex supina* coenopopulations are fully vegetative, whereas in *Galium ruthenicum* seed progeny are sparse but on some sites it may prevail over vegetative progeny.

We shall consider the behaviour of *Carex supina* coenopopulations in some detail. The plant is a system of partial tufts connected by rhizomes. The partial tuft is formed in the apical part of the rhizome by tillering. Its development can be divided into a few stages (Fig. 13): young, mature and old which correspond on the whole to the development stages described by Kershaw (1973) for clumps of other long-rhizome species. The tuft consists of one, two and three year old vegetative shoots and di- or tricyclic reproductive ones. Most tufts die at 4–5 years of age, but some of them can

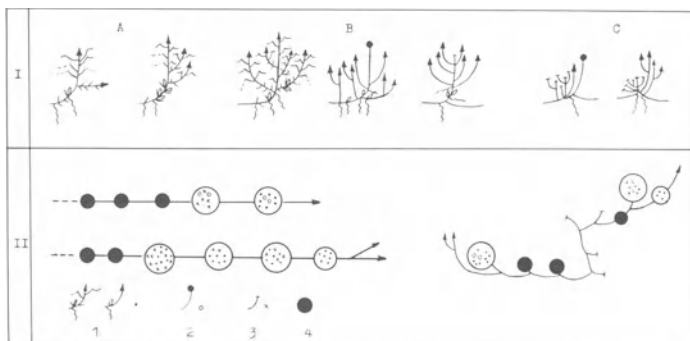


Fig. 13. The phases of development of *Carex supina* partial tufts (I) and structure of individuals. Tufts: A, young; B, mature; C, old. 1, Vegetative shoot; 2, reproductive shoot; 3, dead shoot; 4, dead tuft.

live up to 7 or 8 years. The rhizome is rarely branched and an individual has usually not more than 2–3 rhizome branches (Fig. 13, II). Although reproductive shoots with fruits can usually be seen in a coenopopulation we have never detected seedlings in natural conditions. The coenopopulation dynamics of the species are entirely related to the degree of partial tuft formation and death, both of which undergo changes in time. Sometimes these depend mainly on the weather conditions: the highest number of new tufts is formed in humid years (such as 1973), and these are years when coenopopulation rejuvenation occurs. Young tufts develop rapidly and correspondingly the number of this age-state rapidly decreases in subsequent year. Unless continual formation of young tufts occurs the population undergoes gradual ageing. Most tufts (mainly the old ones) die off in drought years (such as 1975). Since the life-span of tufts is not long the half-life of coenopopulations is short, between 1.1 and 4.0 years depending

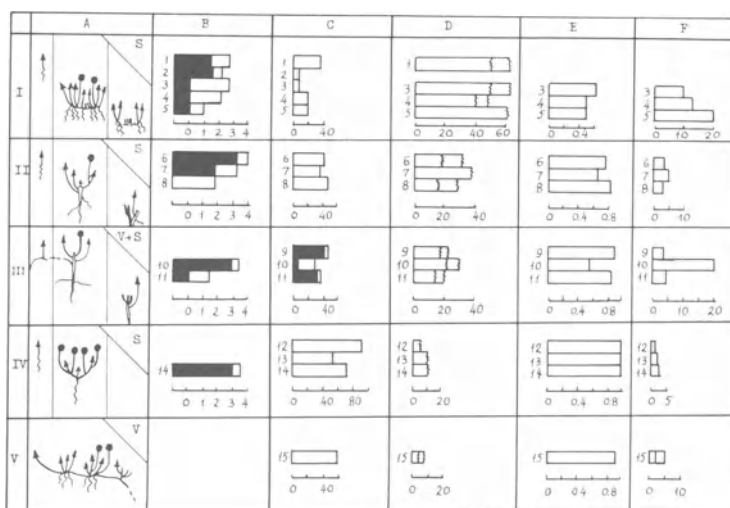


Fig. 14. Some quantitative and qualitative characteristics of the different types (I–V) of population life-history discussed in this paper.

(A) Life-form: arrows, vegetative shoots; arrows with circles, reproductive shoots; heavy black lines, dead shoots. Type of self-maintenance is shown in the upper right corner: s, seminal; v, vegetative.

(B) Seed production per plant (genet), on a logarithmic scale: open columns indicate potential seed productivity, the closed columns, actual seed productivity.

(C) Coenopopulation provision for regrowth, indicated by the number of juvenile and immature plants as a % of the total number; open columns indicate seed progeny and the closed columns indicate vegetative progeny.

(D) Duration of the ontogeny (years).

(E) Balance lability.

(F) Half-life of coenopopulation (years).

1, *Potentilla cinerea*; 2, *Centaurea sibirica*; 3, *Koeleria macrantha*; 4, *Festuca beckeri*; 5, *Stipa pennata*; 6, *Artemisia campestris*; 7, *Onosma simplicissimum*; 8, *Euphorbia seguieriana*, 9, *Helichrysum arenarium*; 10, *Seseli ledebouri*; 11, *Scorzonera ensifolia*; 12, *Syrenia sessiliflora*; 13, *Alyssum tortuosum*; 14, *Alyssum lenense*; 15, *Carex supina*.

on environmental conditions. This factor accounts also for the observation that most partial tufts in coenopopulations were renewed during our observation period (1970–1979): the balance lability was 0.94. The coenopopulations of this species are characterised by a relatively high dynamics of number and age-state composition of partial tufts. The main causes of lability are: (a) sporadic formation of partial tufts, (b) their rather high death rate and (c) their relatively rapid ontogenetic development. Coenopopulations of *Carex supina* are extremely persistent because of their high lability: the species has the ability to utilize rapidly the favourable conditions that occur occasionally in the dry steppes.

CONCLUSIONS

The demographic analysis of steppe plants has shown that a plant community consists of coenopopulations with different types of dynamic behaviour. Some quantitative and qualitative characteristics of the five types considered in this paper are summarised in Fig. 14. In species whose coenopopulations are maintained by seeds (Types I–IV), the following parameters increase from Type I to Type IV: (a) potential and actual seed productivity, (b) the participation of juveniles in the populations, (c) the turnover rate (dynamics of numbers) and correspondingly plant death rate. The duration of plant ontogeny is reduced in the same sequence.

In this paper we have attempted to review some representatives of the diverse types of population biology that may be observed among species living together in a plant community. Since, as we believe, plant morphology and ontogenetic development largely account for the population behaviour of species, the thorough investigation and description of plant life cycles using the insights and techniques of plant morphology are indispensable to population studies (Serebryakov 1962, White 1979). These studies promise to reveal the manner in which plant communities are structured as integrated living systems.

REFERENCES

- (English translations of Russian-language titles are given in brackets)
 Bedanokova, O.A., Vorontzova, L.I. and Mikhailova, N.F. (1975) (Some specific biological features of *Stipa pennata* L. in the steppes of Naurzum reserve.) Bull. Mosk. obsch. isp. prir. otd. biolog. 80(2): 77–91.
 Bespalova, Z.G. and Borissova, I.V. (1979) (Germination peculiarities of caryopsis of *Stipa* L. (Poaceae).) Botan. zhur. SSSR. 64(8): 1081–1090.
 Borissova, I.V., Bespalova, Z.G. and Popova, T.A. (1976) (Peculiarities of phaeological development in plants of steppe and desert associations in northern Gobi (MPR).) Trudy Mosk. obsch. isp. prir. 42: 239–256.
 Borissova, I.V. and Popova, T.A. (1971) (Age phases of bunch-formation in steppe grasses.) Botan. zhur. SSSR. 56(5): 619–626.
 Borissova, I.V. and Popova, T.A. (1972) (The dynamics of quantity and age composition of bunch grass coenopopulation in desert steppes of Central Kazakhstan.) Botan. zhur. SSSR. 57(7): 799–793.

- Gatsuk, L.E., Smirnova, O.V., Vorontzova, L.I., Zaugolnova, L.B. and Zhukova, L.A. (1980) Age states of plants of various growth forms: a review. *J. Ecol.* 68: 675–696.
- Golubev, V.N. (1959) (On some characteristics of the life-form morphogenesis in the herbaceous plants of the forest-meadow zone as related to the evolution of these plants.) *Botan. zhur. SSSR.* 44(12): 1704–1716.
- Golubev, V.N. (1970) (About elementary structural unit of plant communities and its dynamics.) “Mosaic structure of plant communities and its dynamics”, 83–85. Vladimir.
- Golubeva, I.V. (1964) (Age composition and number dynamics of feather-grass (*Stipa pennata* L.) in meadow steppe.) *Uch. zap. Mosc. oblast. pedagog. inst.* 153: 283–303.
- Gordeyeva, T.K. (1976) (Phytomass.) “Main plant communities of Central Kazakhstan desert steppe”, 64–68, Leningrad: Nauka.
- Gorshkova, A.A. and Kopytova, L.D. (1977) (The water reserve in community and expense on the plant transpiration.) “Ecology and pasture degression of steppe communities in Transbaical region”, 53–94, Novosibirsk: Nauka.
- Grigorjev, U.S. and Razumova, L.M. (1974) (Comparative-ecological study of two species of *Festuca*.) *Biolog. nauk.* 8: 73–78.
- Grime, J.P. (1978) Interpretation of small-scale patterns in the distribution of plant species in space and time. pp. 101–124 in A.H.J. Freysen and J.W. Woldendorp (Eds.) *Structure and Functioning of Plant Populations*. Amsterdam, Oxford, New York: North-Holland Publ. Co.
- Grubb, P.J. (1977) Maintenance of species richness in plant communities: the importance of regeneration niche. *Biol. Rev.* 52: 107–145.
- Harper, J.L. 1977. *Population Biology of Plants*. London: Academic Press. 892 pp.
- Ivashin, D.C. and Chuprina, T.T. (1976) (Some biomorphological peculiarities of pinnate feather-grasses in Donbass, with introduction.) “Plant resource of Ukraine, their utilization and enrichment”, 58–62. Kiev. (in Ukrainian).
- Karamysheva, Z.V. and Rachkovskaja, E.I. (1973) (Botanical geography of the Central Kazakhstan steppe zone.) Leningrad: Nauka.
- Kershaw, K.A. (1973) *Quantitative and Dynamic Plant Ecology*. London: Edward Arnold.
- Kolpikov, D.I. (1960) (About some characteristics of the plant response on drought in phytocoenosis of arid steppe.) “Physiology of Plant Stability”. Nauka.
- Kozhevnikova, N.D. and Trulevich, N.V. (1971) (Dry steppes of Inner Tyan-Shan.) Frunze.
- Lavrenko, E.M. (1940) (The steppes of USSR.) “The Vegetation of USSR” 2. Moscow, Leningrad.
- Lavrenko, E.M. (1954) (The steppes of Euroasian region, their geography, dynamics, history.) “The question of botany”, I: 157–191. Moscow, Leningrad.
- Levina, R.E. (1956) (About modes of plant dispersion in steppes.) *Botan. zhur. SSSR.* 45(5): 619–633.
- Mikhailova, N.F. (1977) The great life cycle of *Festuca beckeri* (Hack.) Trautv. in the steppes of the Naurzum Preserve. *Bull. Msk. obsch. isp. prir. biolog.* 82(2): 125–132.
- Osynchuk, V.V. and Shupranov, N.P. (1978) (Seed productivity and seed yield of some sod grasses in phytocoenoses of the Khomutovan steppe.) *Ukrain. botan. zhur.* 35(2): 122–126. (in Ukrainian).
- Persikova, Z.I. (1959) (The formation and life cycle of some tussock grasses.) *Biolog. nauk.* 3.
- Ponomarev, A.N. and Zvorygina, L.F. (1949) (About biology of feather-grasses.) *Uch. zap. Molotov. univer.* 5(1): 63–75.
- Rabotnov, T.A. (1978) On coenopopulations of plant reproducing by seeds. pp. 1–26 in A.H.J. Freysen and J.W. Woldendorp (Eds.) *Structure and Functioning of Plant Populations*. Amsterdam, Oxford, New York: North-Holland Publ. Co.
- Ramenskii, L.G. (1925) (The main regularities of plant cover and their study on the base of geobotanical researches in Voronezh region.) Voronezh.
- Ramenskii, L.G. (1938) (Introduction to complex soil-geobotanical research of lands.) Moscow.
- Sarukhán, J. (1978) Studies on the demography of tropical trees. pp. 163–184 in P.B. Tomlinson and M.H. Zimmermann (Eds.) *Tropical Trees as Living Systems*. London, New York, Melbourne: Cambridge University Press.
- Semenova-Tyan-Shanskaya, A.M. (1978) (Protection regime of herbal communities and individual plant species.) *Zhur. obsch. biol.* 39(1): 3–47.

- Serebryakov, I.G. (1962) (Ecological morphology of plants.) Moscow: Vysshaja shkola.
- Smirnova, O.V., Zaugolnova, L.B. and Ermakova, I.M. (1976) (Plant Coenopopulations: Basic Concepts and Structure.) Moscow: Nauka. 216 pp.
- Solntzeva, M.P. (1968) (The peculiarities of flowering and embryology of feather-grasses.) Uch. zap. Ulyanov. pedagog. inst. 23(3): 29–40.
- Spivak, A.I. (1977) (The potential intensity of photosynthesis of xerophytes in Transbaikalian steppes.) "Ecology and pasture degeneration of steppe communities in Transbaikalian region", 95–123, Novosibirsk: Nauka.
- Stechenko, A.P. (1976) (On relation between live and dead parts of plants in the Pamir highlands.) Ecologia 6: 27–34.
- Sveshnikova, V.M. (1979) (The dominants of Kazakhstan steppes.) Leningrad: Nauka.
- Sveshnikova, V.M. and Bobrovskaya, N.I. (1973) (Ecology of *Stipa* species in Kazakhstan (result of water regime study).) Problems of biogeocoenology, geobotany and plant geography, 240–256.
- Uranov, A.A. (1967) (Ontogeny and age-state composition of populations.) "Age-state composition of flowering plant populations in connection with ontogeny", 3–8. Moscow: Nauka.
- Uranov, A.A. (1975) (Age spectrum of the phytocoenopopulation as a function of time and energetic wave processes.) Biolog. nauk. 2: 7–34.
- Uranov, A.A., Zaugolnova, L.B. and Smirnova, O.V. (1977) (Plant coenopopulations: development and interrelations.) Moscow: Nauka. 134 pp.
- Vasilevich, V.I. (1969) (Statistical methods in geobotany.) Leningrad: Nauka.
- Vorontzova, L.I. and Zhukova, L.A. (1977) (The biomorphological peculiarities and age-state structure of coenopopulations of firm tussock grasses.) Plant coenopopulations: basic conceptions and structure, 107–129. Moscow: Nauka.
- White, J. (1979) The plant as a metapopulation. Ann. Rev. Ecol. Syst. 10: 109–145.
- Zaugolnova, L.B. (1976) (The heterogeneity of coenopopulation in time and space (exemplified by *Alyssum lenense* Adam.)) Botan. zhur. SSSR. 61(2): 177–196.
- Zaugolnova, L.B. (1977) (Analysis of plant coenopopulations as a method of studying anthropogenic effects on phytocoenoses.) Botan. zhur. SSSR. 62(12): 1767–1780.
- Zhuravleva, N.A. (1977) (Interrelation between some ecological and biomorphological indices of steppe plants.) "Ecology and pasture degeneration of steppe communities in Transbaikalian region", 124–152. Novosibirsk: Nauka.