# Handbook of vegetation science

The population structure of vegetation Edited by J. White



Springer-Science+Business Media, B.V.



M. Parfamyob

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.

# STRUCTURE AND DYNAMICS OF COENOPOPULATIONS OF SOME TEMPERATE GRASSES

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# ABSTRACT

The coenopopulation age-state structure of five species of meadow grasses in a variety of coenoses is described. The mode of coenopopulation self-maintenance in different coenoses varied with each of the species, *Deschampsia caespitosa*, *D. flexuosa*, *Festuca pratensis*, *Agropyron repens* and *Poa annua*: seed reproduction alone, a combination of seed and vegetation reproduction, or a predominance of vegetative reproduction. The most persistent species are able to change their coenopopulation age-state spectra in response to changing ecological conditions.

## INTRODUCTION

The duration of any phytocoenosis is determined by the life time of its constituent coenopopulations. This in turn depends on the potential ontogeny and persistence of plants with different life-forms and on the conditions which ensure self-maintenance of coenopopulations. Regular grazing or mowing or flooding are the basis limiting factors hindering such life forms as trees and shrubs in meadow phytocoenoses. Owing to anthropogenic influences secondary meadows dominated by perennial herbaceous mono- and polycarpic plants with a continuously renewable overground shoot system may develop on flood-plain terraces. The minimum and maximum durations of their ontogeny are 1-10 and 50-80 years respectively, that is, considerably shorter than most trees and many shrubs. Meadow phytocoenoses develop more rapidly but are shorterlived than climax forest communities. They are also more dynamic, since they respond quickly to abrupt fluctuations of various exogenous factors. Grasses are typical of these coenoses in the temperate zone, and there have been numerous studies on their ontogeny and on their biological and ecological characteristics (Rozhevitz 1937, Smelov 1947, Larin 1950, Serebryakova 1971, Tsvelev 1976, Arber 1934). However demographic characteristics have been obtained for only a few species of grasses. The object of this study is to show the diversity of coenopopulation structure and modes of self-maintenance for a number of grass species and to describe the basic features of their life cycles which account for the dynamic processes of phytocoenoses.

Individuals of a coenopopulation have various calendar ages, agestates, sexual and other biological characteristics. Studies now completed on over 200 species of flowering plants, including 60 meadow species, have confirmed the method of age-state definition for different life-forms (Smirnova et al. 1976, Uranov et al. 1977).

## MATERIALS

Grasses of different life-form, characterised by different types of growth and coenopopulation self-maintenance were studied (Fig. 1): *Deschampsia caespitosa* P.B. (tussock grass), a compact caespitose meadow weed; *Festuca pratensis* Huds. (meadow fescue), a loose caespitose grass of high feed value; *Deschampsia flexuosa* Trin. (common hairgrass), a caespitosestoloniferous grass of medium feed value; *Agropyron repens* L. (couch grass), a long-rhizome valuable meadow grass; *Poa anna* L. (annual meadow grass), a short-lived pasture grass of medium feed value. Meadow fescue was studied by Ermakova (1968), the other four species by Zhukova (1961, 1979, 1980).

According to the accepted subdivision of age-state ontogeny (Rabotnov 1950a, Uranov 1975, Gatsuk et al. 1980), the species were classified into 9 or 10 age-states (full details in Serebryakova 1980). Coenopopulations of the species were studied on the inundation and continental meadows in the northern, north-western and central regions of the European part of the USSR, and on the mountain meadows of the Trans-Carpathian area and the Crimea. Details of the ecology and management of the various habitats investigated are given in Tables 1–5. All the individuals collectively of a species in a particular site (phytocoenosis) belong to one type of coenopopulations encountered in various habitats is indicated on the tables: their precise definition will be presented later. Over 70 coenopopulations of *D. caespitosa* were examined, together with 44 of *F. pratensis*, 21 of *D. flexuosea*, 12 of *A. repens* and 10 of *P. annua*.

In order to characterise each population 25-300 plots, each  $0.25 \text{ m}^2$  in area, were established. For dynamic studies on the coenopopulations of tussock-grass, common hairgrass, meadow fescue and annual meadow-grass, the same coenoses were inspected for a number of years. The age-states of individuals of each species were determined on temporary or permanent plots. Absolute and relative participation of each age-state group and the coenopopulations age-state spectrum were calculated for each phytocoenosis. Averaged spectra for similar climatic conditions or similar types of pasture utilization were also calculated. Detailed methods are given in Smirnova et al. (1976).



Fig. 1. Schematic diagram of age-states in the ontogeny of four grasses: (a) Deschampsia caespitosa, (b) Deschampsia flexuosa, (c) Festuca pratensis, (d) Agropyron repens. The ontogeny of Poa annua resembles (c). A horizontal projection of the tussocks is given in the upper part of the diagram for D.caespitosa. 1, caryopsis; 2, coleoptile; 3, adventitious roots; 4, assimilating leaves; 5, rosette shoot; 6, reproductive semi-rosette shoot; 7, tussock live part; 8, partial shoot, 9, offshoot; 10, communication rhizomes; 11, dead shoot; 12, decayed part.

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Coenopopulation type	Region	Dominants	Richness in species (grasses + legumes + forbs)	Number of layers	Total cover %	Cover projected %	Total crop gm <sup>-2</sup>	% Share in crop	Management
Invasive	Moscow region, Carpathians	1	10-70	1-2	25-30	<ul><li>√</li><li>5</li></ul>			Paths for cattle, trampled area 1–2 years old, summer cutting
Normal young	Moscow region, Carpathians	Deschampsia caespitosa, Festuca pratensis, Trifolium repens, Ranunculus acris, Ranunculus	$\begin{array}{c} 53\\ (29-100)\\ (10+5+38)\end{array}$	т	73	25	348-657	10-12	Improved pastures, 6–8 years old pastures, 2–5 years old felled area, 10 years old artines of surrice
mature	Flood lands of Oka and Severnaya Dvina, Carpathians, Vologda region, Moscow region, Karelian ASSR	Deschampsia Deschampsia caespitosa, Festuca pratensis, Ranunculus acris, Trifolium repens	34 (8 + 3 + 23)	m	79	30	209-613	9–35	6–30 years old pastures, hay meadows of Oka and Severnaya Dvina rivers, subalpine meadows of the Carpathians, dry meadows, 5–10 years old felled area

Table 1. Phytosociological and ecological characteristics of coenoses with Deschampsia caespitosa.

35-40 years old perennial pastures flood plain mainland hay meadows, 10-20 years old felled area, birch forests	Mainland and flood plain hay meadow, aspen forests, pastures, terraces
5.5–34	2.7
250-1370	120–335
24	و
78.2	83
<del>4</del>	б 4
$\begin{array}{c} 37\\ (19-50)\\ (8+4+25)\end{array}$	(9 + 5 + 28)
Deschampsia caespitosa, Festuca rubra, Agrostis stolonizans, Ranunculus acris, Trifolium repens, Alchemilla vulgaris	Deschampsia caespitosa, Agrostis stolonizans, Poa trivialis, Ranunculus repens
Flood lands of Oka and Severnaya Dvina, Moscow region, Vologda region, Karelian ASSR	Flood lands of Oka, Karelian ASSR, Kaluga region, Vologda region
ageing	old

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Coenopopulation type	Region	Dominants	Richness in species	Number of layers	Total cover %	Cover projected %	Management
Invasive	Arkhangelsk region Pribaltik	Deschampsia flexuosa, Epilobium angustifolium	29 (20–37)	1-2	43	×	1-2 years felled area
Normal							
young	Karelian ASSR Pribaltik Arkhangelsk region	Picea excelsa, Deschampsia flexuosa, Epilobium angustifolium	20 (15–38)	2–3	60	22	Felled area, grass heath, plantings of pine and spruce forest
mature	Pribaltik	Pinus silvestris, Deschampsia flexuosa	16 (15-20)	4	70	30	Plot of natural park
ageing	Arkhangelsk region Jaroslavl region Karelian ASSR	Deschampsia flexuosa, Vaccinium myrtillus, Nardus stricta	12 (7–22)	3–5	75	32	Felled area, plantings of spruce, island grass heath
old	Karelian ASSR Jaroslavl region Arkhangelsk region	Picea excelsa, Vaccinium vitis-idaea, Deschampsia flexuosa, Nardus stricta	17 (13–22)	3-4	60	14	Felled area, island grass heath, plantings of pine and spruce
Regressive	Moscow region	Pinus silvestris Festuca ovina, Deschampsia flexuosa	15	ŝ	80	10	Plantings of pine

Table 2. Phytosociological and ecological characteristics of coenoses with Deschampsia flexuosa.

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Coenopopulation type	Region	Dominants	Richness in species (grasses + legumes + forbs)	Number of layers	Total cover %	Cover projected %	Total crop gm <sup>-2</sup>	% Share in crop	Management
Invasive	Pscov region	1	I	I	I	I	118 (86–150)	2.7–59	Hay meadows (1 cutting)
Normal young	Pscov region	Dactylis glomerata Festuca pratensis Taraxum officinale	33.7 (8.4 + 3 + 22.3)	4	73	3.5	143 (97–170)	5-48	Hay meadow (3 cuttings)
mature	Moscow region Kaluga region Crimea	Festuca pratensis	42.6 (8.8 + 3.4 + 30)	4	76	37.7	67	31	Hay meadow (lc.), mowing and grazing combined
ageing	Kaluga region Arhangelsk region Rjasan region Karelian isthmus	Festuca pratensis F.rubra	40.0 (8.1 + 4.2 + 27.7)	4-5	8	11.5	(1.5–425)	1.3–29	Hay meadow (1c.), mowing and grazing combined + pasture meadow (3 cuttings)
old	Kaluga region Moscou region Rjasan region Crimea Karelium isthmus	Festuca pratensis F.rubra Zerna inermis Poa pratensis P.augustifolia	43.7 (8.1 + 4.6 + 31)	4-5	77	9.6	27 (5.6–61)	2.5-14.9	Hay meadow (1-3 cuttings) meadow pasture

Table 3. Phytosociological and ecological characteristics of coenoses with Festuca pratensis.

Coenopopulation type	Region	Dominants	Richness in species	Numbers of layers	Total cover %	Cover projected %	Total crop g m <sup>-2</sup>	% Share in crop	Habitat
Invasive Normal young	Kaluga region Moscow region Ural	Agropyron repens, Agropyron repens, Festuca pratensis, Deschampsia caespitosa, Trifolium repens	27 (25–30)	2-3	50-80	10-12	121-1725	6.6–32	Meadow of intensive use (Oka), fallows, flood-plain pastures
mature	Moscow region Kaluga region	Agropyron repens, Festuca rubra, Trifolium repens	18 (10-24)	2–3	70-85	20–25	361	5-27.5	Fallows, hay dry meadows
ageing	Kaluga region Pskov region Karelia ASSR	Agropyron repens, Festuca pratensis Dactylis glomerata	21 (17–30)	2–3 2–3	90-100	12-16	570842	3.5-15	Meadow of intensive use (Oka), sown meadows (Karelian ASSR)
old	Moscow region Ural Pskov region	Agropyron repens, Festuca pratensis, Deschampsia caespitosa, Trifolium repens	23 (15–27)	2–3	06-02	8-10	616-1376	1.2-11	Fallows, flood-plain pastures, sown meadows

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Table 5. Phytosoc	iological and eco	logical characteristics of	coenoses with	Poa annua.					
Coenopopulation type	Region	Dominants	Richness in species	Number of layers	Total cover %	Cover projected %	Total crop g m <sup>-2</sup>	% Share in crop	Management
Invasive	Moscow region	Taraxacum officinale, Plantago major, Polygonum aviculare, Tripleurospermum inodorum	10-15	1–2	20-25	S			Fallow, sown meadow, dry meadow
Normal young	Moscow region	Poa annua, Agrostis tenuis, Plantago major, Taraxacum officinale	6-16	7	30-42	10-12	24-97	4.8–5.5	Fallow, sown meadow, dry meadow, roadsides
mature	Moscow region	Poa annua, Festuca pratensis, Plantago major	6-15	2–3	40-50	25	57-75	10.7–32	Fallow, dry meadow
ageing	Moscow region	Poa annua, Festuca pratensis, Poa pratensis, Taraxacum officinale	5-12	2–3	60-70	20-25	20-60	1.5–19	Fallow, dry meadow, roadsides
blo	Moscow region	Poa annua, Festuca pratensis	3-5	1–2	40	10-15	74-111	0.13–2	Dry meadow

# AGE-STATE SPECTRA OF COENOPOPULATIONS

Coenopopulations of any species may be considered as continously developing elements of the plant cover (Uranov 1975). The comparison of age-state spectra of the same (single) species in different meadow phytocenoses shows a wide range, caused primarily by different stages in their development. Rabotnov (1969) proposed a classification of coenopopulations into three types: invasive (I), normal (N) and regressive (R) to correspond with their long term development from emergence to maturity and to extinction. The unidirectional development of a coenopopulation ranging from the invasive to regressive state constitutes the 'large life cycle' (Rabotnov 1969) of the coenopopulation or 'big wave of population flow' (Uranov and Smirnova 1969); the development of one diaspore generation from invasion to death constitutes a 'small or reproduction wave' (Smirnova et al. 1976).

The types of coenopopulations of the various grasses we have studied are summarized in Tables 6-10 and will be discussed below in turn for each species.

#### (a) Invasive coenopopulations

Invasive coenopopulations consist of plants of the pregenerative period and are incapable of self-maintenance since they depend on continual diaspore invasion. Coenopopulations of this type are rather rare in meadow phytocoenoses and occur mainly on plots with a highly disturbed plant cover (pastures, cattle tracks) or on primary substrates such as alluvial deposits in flood-plains, spoil banks of irrigation or drainage systems, as well as in the first stages of meadow agrophytocoenoses.

Invasive coenopopulations of *D.caespitosa* constituted 6.3% of all coenopopulations of this species which we studied. They were found in cattle camps of high-mountain meadows in the Trans-Carpathian area, on cattle tracks of Oka pastures, and in the annual meadowed felling areas of forests. These invasive coenopopulations emerge either in sites of old overgrazed coenopopulations or on formerly unoccupied places such as forest felling areas. They may develop from seed (caryopsis) reserves in the soil or be dispersed from elsewhere. According to Rabotnov (1950b) the number of caryopses in soil was  $20-100 \text{ m}^{-2}$  in the central flood-plain and  $220 \,\mathrm{m}^{-2}$  in terrace-side areas. The invasive coenopopulation density is rather variable (Table 6). The first months are marked only by seedling emergence, then come the juvenile plants and after 2-4 years the age-state spectrum is represented by all groups of the pregenerative period. The phytocoenotic significance of these coenopopulations is low since their projected cover is only 1-5% (Table 1). The negative effects of various exogenous factors result in continuous elimination of young D. caespitosa plants and cause distinct fluctuations in the population density of all age-states groups present, particularly the seedlings. The death of the whole coenopopulation is not infrequent. Such doomed coenopopulations

Table 6. Coenopo	pulation chai	racteristics of	Deschampsia caespit	osa. The values	of some param	sters are shown a	s means (a	nd ranges).
Coenopopulation type	Age-state groups*	Duration of life (vears)	Coenopopulation age level	Population density	Quantity of generative individuals	j + v $g_1 + g_2 + g_3$	Recorde	1 Habitat es
		(Jears)		(_mcz.u.ad)	11111111111111111111111111111111111111	(%)	S N	of ial
Invasive	p, j, v	2-5	0.05 (0.03-0.09)	72.25 (3.1–177.0)	0	1	4	.3 Paths for cattle, trampled areas, 1–2 year-old summer cutting
(i) young	j, v, <u>81</u> , 82, 8 <sub>3</sub> , (SS, S)	3-5	0.28 (0.09–0.35)	6.1 (2.7–15.2)	52.9 (48.2–57.7)	183 (24–945)	9 14	<ul> <li>Improved pastures,</li> <li>6-8 year-old pastures,</li> <li>2-5 year-old felled area</li> <li>10 year-old spruce</li> <li>plantation</li> </ul>
(ii) mature	(j), v, g <sub>1</sub> , <u>g2</u> , g3, ss, (s)	12-20	0.49 (0.27–0.63)	4.0 (2.38–8.6)	67.0 (64.8–68.6)	50 (4-96)	26 40	.6 6–30 year-old pastures and hay meadows of Oka S. Dvina rivers, subalpine meadow, dry meadows, 5–10 year felled area
(iii) ageing	(j, v), $g_1$ , $g_2$ , $\frac{g_3}{g_3}$ , (ss, s)	8–15	0.59 (0.53–0.72)	3.56 (2.0–7.2)	70.3 (64.4–75.9)	27 (1–85)	17 26	.6 35-40 year-old perennial pastures, flood-plain main land hay meadows, 10-20 year-old felled area, birch forests
blo (vi)	(j, v, g <sub>l</sub> ), 82, g <sub>3</sub> , <u>ss</u> , (s)	5-15	0.53 (0.41–0.80)	2.1 (1.6 4.9)	39.3 (32.9–43.4)	81 (12-208)	8 12	.5 Mainland and flood-plain hay meadows, aspen forests, pastures, terraces
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\*The predominating age-state group is underlined and groups which may be absent are shown in brackets.

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Coenopopulation type	Age-state groups*	Duration of life	Coenopopulation age level	Population density	Quantity of generative	$\frac{\mathbf{j} + \mathbf{i}\mathbf{m} + \mathbf{v}}{\mathbf{g}_1 + \mathbf{g}_2 + \mathbf{g}_3}$	Reco	rded ences	Habitat
		(years)		(per 0.20 m <sup>-</sup> )	1110111111111	(%)	z	% of total	
Invasive	p, j, im, v	1–3	0.006 (0.003–0.020)	85.2 (31.7–171.7)	0	1	9	20	1-2 years felled area
Normal (i) young	p, j, im, v <u>g,</u> g <sub>2</sub> (g <sub>3</sub> , <u>ss</u> s)	2–3	0.21 (0.15–0.34)	10.9 (3–25)	14.7 (9.4–25.9)	417.8 (59–832)	9	20	Felled area, grass heath, plantings of pine forest
(ii) mature	$(p, j, im), (v), g_1, g_2, g_2, g_3, (ss, s)$	1–2	0.43	4.4	42.9 (40–45.7)	59.0	4	13.3	Plot of natural park
(iii) ageing	(p, j, im, v, g <sub>1</sub> ), g <sub>2</sub> , <u>g<sub>3</sub></u> , ss (s)	7–12	0.60 (0.45–0.78)	4.36 (2-16)	34.0 (18.3–77.8)	42.0 (27–72)	6	20	Felled area, plantings of spruce, island grass heath
(iv) old	ы, (д. р. ј. im, v, 81, 82, 83, SS, S	3-5	0.73 (0.41–0.87)	5. (1.3–12.8)	15.2 (6.8–25.0)	20.7 (8.1–63)	٢	23.4	Felled area, island grass heath, plantings of pine and spruce
Regressive	1	2-?	0.89	1.75	0	0	I	0.3	Plantings of pine
*The predominating	age-state group is	underlined an	d groups which may be	: absent are showr	ı in brackets.				

Table 7. Coenopopulation characteristics of Deschampsia flexuosa. The values of some parameters are shown as means (and ranges).

Coenopopulation type	Age-state groups*	Duration of life	Coenopopulation age level	Population density	Quantity of generative	$\frac{\mathbf{j} + \mathbf{i}\mathbf{m} + \mathbf{v}}{\mathbf{g}_1 + \mathbf{g}_2 + \mathbf{g}_3}$	Reco	rded ences	Habitat
		(ycars)	(7)	(per 0.2.m <sup>-</sup> )	11111111111	(%)	z	% of total	
Invasive Normal	p, j, im, v	-	0.6 (0.04–0.09)	175.7 (17–252)	0	Ι	16	16.6	Agrophytocoenoses Pscov region
(i) young	p, j, im, v, <u>g</u> 1, g2, (g <sub>3</sub> , ss, s)	0.1-1	0.19 (0.18–0.29)	6.6 (3.1–11.1)	51.32 (20–73)	54.45 (12–158)	16	16.6	Agrophytocoenoses Pscov region
(ii) mature	(p, j, im, v), $g_1, g_2, g_3,$ (ss, s)	1-5	0.45 (0.28–0.67)	11.01 (0.4–27.5)	45.41 (22–54)	51.39 (34–78)	4	5.7	Flood-plain of Ugra River, mountain meadow (Crimea), dry meadow (Karelian)
(iii) ageing	(p, j, im, v, g. <sub>1</sub> ), (g <sub>2</sub> ), <u>g.</u> 3, ss, (s)	4	0.67 (0.28–0.98)	4.5 (1.3-9.9)	64.82 (36–85)	10.58 (0–98)	1	24.2	Flood-plain of Ugra River, Oka River, Severnaya Dvina River, Severnaya Dvina River, dry meadow (Karelian), mountain meadow (Crimea)
(iv) old	(p, j, im, v, g <sub>1</sub> ), (g <sub>2</sub> ), g <sub>3</sub> , <u>ss</u> (s)	1-13	0.75 (0.42–0.97)	5.5 (2–14.5)	27.78 (9-45)	22.88 (0-100)	17	24.2	Flood-plain of Ugra River, Oka River, Severnaya Dvina River, mountain neadow (Crimea), dry meadow (Karelian, Moscow region)

Table 8. Coenopopulation characteristics of *Festuca pratensis*. The values of some parameters are shown as means (and ranges).

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Coenopopulation type	Age-state groups*	Duration of life	Coenopopulation age level	Population density	Quantity of generative	$\frac{\mathbf{j} + \mathbf{i}\mathbf{m} + \mathbf{v}}{\mathbf{g}_1 + \mathbf{g}_2 + \mathbf{g}_3}$	Recor	ded	Habitat
		(years)	(9)	(per 0.25 m <sup>-</sup> )		(%)	z	% of total	
Invasive									
young	(j, im, v), <u>81</u> , 82, (g., SS, S)	12	0.31 (0.15–0.44)	90.2 (32–191)	29 (20.9–50)	234 (45-400)	5	31.3	Meadow of intensive use (Oka), fallows, flood-plain pastures
mature	(j, iii), v, 1, 100, v	0.5–3	0.47 (0.43–0.54)	72.0 (70.2–129)	53.2 (46.5–59.7)	44.3 (2 <del>5</del> –59)	e	18.7	Fallows, hay dry incadows
ageing	<b>(j, im, v),</b> <b>g</b> <sub>1</sub> , <b>g</b> <sub>2</sub> , <b>g</b> <sub>3</sub> , (ss, s)	1-2	0.54 (0.44-0.65)	51.3 (39–60)	78.0 (53.8–100)	6.6 (0–10.1)	ς.	18.7	Meadows of intensive use (Oka), sown meadows (Karelian ASRR)
old	(im), v, g <sub>1</sub> , g <sub>2</sub> , g <sub>3</sub> , <u>ss</u> , (s)	0.5–1	0.55 (0.46–0.68)	75.8 (25–198)	25.1 (13.6–43.5)	182.5 (8.4–363)	S	31.3	Fallows, flood-plain pastures, sown meadows

Table 9. Coenopopulation characteristics of Agropyron repens. The values of some parameters are shown as means (and ranges).

\*The predominating age-state group is underlined and groups which may be absent are shown in brackets.

Coenopopulation type	Age-state groups*	Duration of life (vears)	Coenopopulation age level (A)	Population density	Quantity of generative individuals	$\frac{j + im + v}{g_1 + g_2 + g_3}$	Reco	orded rences	Habitat
			(mean)	(mean)	%	(%)	z	% of total	
Invasive	p, į, im, v	0.5-1	0.025	138.2	0	1	e	18.7	Fallow, sown meadow, dry meadow
Normal young	j, im, v, <u>g1</u> , (g <sub>2</sub> ), (g <sub>3</sub> , sc)	0.5–2	0.24	40.6	22.6	602.5	٢	43.8	Fallow, sown meadow, dry meadow, roadsides
mature	∞) (j, im, v, g₁), g₂, g₃,	0.5–1	0.31	26.5	68.4	49.1	7	12.5	Fallow, dry meadow
ageing	м V, g <sub>1</sub> , g <sub>2</sub> , 9., SS, S	0.5–1	0.66	14.2	76.0	1.7	ŝ	18.7	Fallow, dry meadow, roadsides
old	8) 8) 8)	0.5–1	0.84	18.3	8.9	0	-	6.3	Dry meadow
*The predominating	age-state group i	s underlined a	nd groups which may b	oe absent are show	n in brackets.				

Table 10. Coenopopulation characteristics of Poa annua.

of tussock grass occur on alluvial deposits of the Oka and North Dvina rivers, as well as on spoilbanks of drainage ditches.

Invasive populations of *D.flexuosa* are common in forest felling areas and rare on sand dunes. Their population density ranges widely (Table 7) with a cover of 5-8%. However their rate of individual development is high and by the end of the first year the coenopopulation includes all groups of the pregenerative period, and in the second year some of the virginile plants proceed to flower.

The life time of *Poa annua* invasive coenopopulations is even shorter than those of *Deschampsia* (Table 10). Their population density is 57-375 individuals per  $0.25 \text{ m}^2$ .

Invasive coenopopulations were not found either in couch grass or in meadow fescue in natural phytocenoses. However, invasive populations of *Festuca pratensis* lasting for less than one year have been described (Ermakova and Mironova 1980) in meadow agrophytocoenoses in the sowing year; their population density was 17–252 individuals per 0.25 m<sup>2</sup>.

#### (b) Normal coenopopulations

Normal coenopopulations do not depend on diaspore invasion and are capable of self-maintenance by seed or vegetative propagation, either simultaneously or in succession. This is the most frequent coenopopulation type and may be described as 'full-membered' if all age-states are present, or 'incomplete-membered' if one or several groups are absent. The incomplete-membered type can be caused either by the effects of various exogenous factors (climatic, zoogenic, anthropogenic, etc.) resulting in interruption, elimination, delay or acceleration of individual development, by the effects of endogenous factors such as the inhibition of development of young growth by adult plants, or by specific characteristics of flowering and fruit formation in different age-states. The incomplete-membered coenopopulation spectrum can either be related to a natural absence of the postgenerative period in the ontogeny, as in monocarpic plants, or to the relatively young age of a coenopopulation if no plants have reached the ss and s age-states. Spectra without young growth lack reproduction waves. Polymodal spectral reflect different waves of reproduction, possibly due to irregular, non-annual seedling establishment. Age-state spectra are shown graphically with age-states ranked from **pl** to **s** in sequence along the abscissa from left to right; the terms 'left-handed' and 'right-handed' spectra refer to the preponderance of young or of old individuals on such a graph.

Following the concepts of Zhukova (1967) and of Uranov and Smirnova (1969), we classified the normal coenopopulation into four versions according to their successive development stages.

(i) Young normal coenopopulations have the  $\mathbf{g}_1$  age-state group prevalent among adult plants and show a relatively regular replenishment of the adult population. The spectrum is, as a rule, left-handed; this is due to the presence of most or all of the pregenerative age-states predominant over the postgenerative ones.

In *D.caespitosa* this version constitutes about 14% of all coenopopulations studied and was found in 2-3 year old post-felling areas and in 8-10 year spruce plantations (Table 6). These coenopopulations emerged as a result of recent species invasion to these areas and are primarily incomplete-membered, with the oldest ss and s groups being absent. The population density is rather high. Flood pastures are characterized by young, full-membered coenopopulations with a lower population density (3 or 4 individuals per  $(0.25 \text{ m}^2)$  and continuous seed reproduction (Zhukova 1980). The number of young individuals averages about 2 per single generative plant here. This results primarily from coenosis unsaturation with a particular species and is due to the relatively small diameter of the grass tussock (5–10 cm) and area of its influence ('phytogenic field' sensu Uranov 1965) (8.3–115 cm<sup>2</sup>) under the prevalent young generative plants. The openness of the vegetation ensures the persistence of new waves of reproduction and intensive growth of the existing individuals. This results in rapid development of young normal coenopopulations of D.caespitosa, with a life-time no longer than about 2-5 years.

The young normal coenopopulations of *D.flexuosa* were described on waste-land meadows and plots of burned forests (Table 7). The area occupied by one individual in the prevalent  $g_1$  age-state is 10–38 cm<sup>2</sup>. The life-span of individuals is 1–2 years (Zhukova 1979).

The young normal coenopopulations of Agropyron repens are, as a rule, incomplete-membered, being devoid of seedlings and juvenile plants: this is due to the complete inhibition of seed reproduction (Table 9). Young generative and virginile groups with numerous young rhizomes are prevalent. The total number of communication rhizomes linking short clusters or 'partial tufts' (Fig. 1d) is lower than that of the offshoots. The mode of coenopopulation self-maintenance is vegetative and new offshoots are formed by the separate shoot clusters. Coenopopulation density is 5.2 shoot clusters per  $0.25 \text{ m}^2$ . The ageing of these coenopopulations is manifested in the gradual accumulation of  $\mathbf{g}_3$  and  $\mathbf{ss}$  age-states absent in the earlier stages.

In *Festuca pratensis* the young normal coenopopulation was identified in the second year of its occurrence in agrophytocoenoses (Table 8). The coenopopulation was characterised by the prevalence of young generative plants, the presence of virginile and sometimes immature plants, and the emergence of a few medium-aged generative plants a month later; it is quite short-lived.

The young normal coenopopulations of *Poa annua* have a rather high population density (Table 10). Initially individuals of the pregenerative period are prevalent. As the number of generative plants increases the number of seedlings and juvenile plants is drastically reduced.

(ii) Mature normal coenopopulations are characterised by the prevalence of the  $g_2$  age-state group, cover the greatest area in coenoses and produce the highest amount of biomass in these grasses. Their age spectra are uni- or bimodal: the second peak is among the groups of the pregenerative period whose population density is higher than the

postgenerative fraction, and this indicates continual recruitment from seed or vegetative reproduction.

In Deschampsia caespitosa mature coenopopulations are widespread and constitute about 40% of all the coenopopulations of this species studied. Medium-aged generative plants accumulate and result in considerable duration of this age-state, for 5–15 years or longer (Table 6). The stability of mature Deschampsia coenopopulations reflects the competitive ability of  $g_2$  individuals which have large tussocks (10–15 cm diameter) and aggressive root systems (30–40 cm diameter) leading to large phytogenic fields, both under each individual (226–933 cm<sup>2</sup>) and under the group as a whole. Deschampsia caepitosa is a strong edificator and produces an inhibiting effect on other species and on its own young growth.

In *D. flexuosa* mature normal coenopopulations are less frequent (about 10%). The tussock area in the  $g_2$  age-state is 140–270 cm<sup>2</sup>, the phytomass is 6.9–7.3 g and seed reproduction is predominant.

In *Festuca pratensis* this coenopopulation type occurred only rarely in natural phytocoenoses; in the flood-plain of the Ugra River, where it was the dominant species, the projective coverage was about 50-60%. In the adult part of the coenopopulation all groups of generative plants were present with intensive seed reproduction. There were 3.2 group individuals per generative individual. The total population density reached a level of 27 individuals per 0.25 m<sup>2</sup>. In meadow fescue, as in most loose-caespitose grasses, this coenopopulation version is short-lived and is replaced by the ageing one after 1–4 years.

In Agropyron repens the mature coenopopulation was recorded on fallow sites. It was devoid of seed reproduction and particules of vegetative origin were predominant in the  $g_2$  age-state. As a rule the coenopopulation is polycentric with a ratio of offshoots to communication rhizomes close to 1. Separation of non-rejuvenated shoot clusters in the generative state and of rejuvenated ones in the immature and virginile states is possible. A high intensity of vegetative reproduction was recorded.

(iii) The ageing normal coenopopulations are characterised by constant prevalence of age-state  $g_3$ . This type may be subdivided into those with (a) a prevalence of pregenerative plants over the postgenerative ones, and (b) a prevalence of postgenerative plants over the pregenerative ones.

In Deschampsia caespitosa about a quarter of the coenopopulations observed were ageing normal (Table 6). From north to south there is a tendency towards a decrease in their occurrence: they make up 33%, 21% and 16% of the coenopopulation in the northern, central and Trans-Carpathian areas, respectively. Their relative frequency changes only slightly with different modes of grassland utilization. Their generalized spectrum is distinctly single-peaked, with the peak on the  $g_3$  age-group. Large tuft-clones are about 20–30 cm in diameter, consist of 2–5 particules and form a single phytogenic field, 360-1040 cm<sup>2</sup> in area. Rather large groups of dead shoots in tussock-grass tufts retain a high allelopathic activity (Zhukova and Bogdanova 1977). Consequently, in spite of the reduction in the population density (Table 6), the coenotic closure in the

ageing tussock-grass coenopopulations becomes higher and seed reproduction decreases drastically. This is confirmed by the much lower participation of pregenerative plants in coenopopulations (13.5%) and a ratio of young plants per generative individual of 0.23:1. Nearly 50% of the incomplete-membered ageing coenopopulations studied were devoid of juvenile and/or virginile individuals. The postgenerative fraction is somewhat higher, although with intensive grazing senile plants may be absent. Full-membered ageing coenopopulations with weakly manifested reproduction waves occur on hay meadow plots which have a lower level of coenosis occupancy by tussock-grass.

The life time of the ageing tussock-grass coenopopulations is determined in the absence of reproduction waves by the duration of the old generative age-state  $\mathbf{g}_3$ ; it may last from 3 to 15 years and probably longer. The species continues to be an edificator in the ageing tussock-grass meadows in spite of the reduction in its projective coverage by as much as 30-40%.

In *Festuca pratensis* the ageing normal coenopopulations are widely distributed in pastures and rarer in hay meadows. They are co-dominants (in 65% of cases studied) and less frequently (35%) subordinate though permanent members of the coenosis. If reproduction is annual then all age states of the pregenerative period are present in the coenopopulation, otherwise only some of them are present or pre-generative plants are altogether absent. Young, medium-aged and senile plants are few or absent and the ss-group is relatively abundant. Plant size, developmental potential, productivity and projective coverage are lower than in the previous coenopopulation version. The area occupied by the prevalent  $g_3$  individuals is 13.2–34.2 cm<sup>2</sup> each. The number of young individuals per one generative individual ranges from 0.01 to 4.9.

In *Deschampsia flexuosa* four ageing coenopopulations were identified in the meadowed 7–8 year-old felling areas. On the rough meadows of the White Sea Islands they are usually full-membered, less frequently incomplete-membered, by the absence of a number of groups belonging to the pregenerative period; age-state  $g_3$  constitutes 30–56% of the coenopopulation. They cover an area of 514 cm<sup>2</sup>. The total population density is unstable, ranging from 2 to 16 specimens per 0.25 m<sup>2</sup>.

In Agropyron repens ageing coenopopulations are rare and represented by old polycentric systems or single partial tufts in which the number of communication rhizomes is considerably higher than that of the aboveground shoots. As a rule, they occur on perennial old fallow fields.

(iv) The old normal coenopopulations are characterised by the prevalence of subsenile plants and a distinct righthanded age-state spectrum; the population density of the generative plants is lower than that of the postgenerative. Sometimes the co-prevalence of groups ss and  $g_3$  is possible in an intermediate version.

In *Deschampsia caespitosa* old normal coenopopulations occur far less frequently than mature and ageing ones (Table 6): they constitute 5.3% in pastures, 20.8% on haylands and are absent in forest felling areas. Such

uneven occurrence of this type can be explained by the lower viability of the ss group which is fully eliminated by grazing but preserved slightly longer by hay-mowing management. Tussock-grass individuals do not manage to reach the ss age-state in the 10–15 year old felling areas and accumulate mainly after 20–30 years when the felling area is overgrown: thus in forest phytocoenoses old normal coenopopulations occur far more frequently (40%). The total population density of these coenopopulations is low (Table 6). This is associated with a simultaneous decrease in clonetussock areas (to 112–136 cm<sup>2</sup>), primarily in the area under the living part (to 19–70 cm<sup>2</sup>). By this stage there is a decrease in coenosis saturation with tussock-grass, but at the same time there is fresh recruitment of seeds from the seed reserves in the soil. Consquently the share of the pregenerative fraction increases (to 22.6%) and two or three-peak age-state spectra develop.

The old normal coenopopulations of *D. flexuosa* occur most frequently on the island and continental rough meadows and on 12–16 year old felling areas. Their total population density is low (Table 7) and the area of one clone is  $46-394 \text{ cm}^2$ . The coenopopulation is self-maintained by vegetative reproduction; seed reproduction is inhibited.

In *Festuca pratensis* the old normal coenopopulations are widespread in all the investigated geographical localities and habitats. Sporadic groups of pregenerative individuals and  $\mathbf{g}_1$  and  $\mathbf{g}_2$  are either scarce or absent. According to all indicators, this coenopopulation is rather similar to the previous one (Table 8). The area under one individual is  $0.7-1.6 \text{ cm}^2$ . The old normal coenopopulations of meadow fescue are nearly equally frequent as co-dominant and as subordinate components of the communities.

In Agropyron repens the old normal coenopopulations were reported for old fallow fields, roadsides and artificial agrophytocoenoses. All or most of the pregenerative groups are preserved in them, with immature or virginile partial tufts occurring. The saturation of the upper soil layers with communication rhizomes increases.

#### (c) Regressive coenopopulations

Regressive coenopopulations are those that are unable to maintain themselves either through seed or vegetative reproduction and are thus dependent on immigrant diaspores. Three variants are recognised (Smirnova et al. 1976);

 $R_1$  is devoid of viable seed and individuals of the pregenerative period; flowering (but not fruiting) individuals and groups of the postgenerative period are present.

 $R_2$  consists of sub-senile and senile plants.

 $R_3$  consists of senile plants.

Regressive coenopopulations are extremely rare in nature and were not identified in tufted hairgrass, meadow-fescue or couch grass. In common hairgrass only one regressive coenopopulation was reported, near the southern border of its range in a 15 year old pine tree plantation in the Moscow region. This indicates both the low vitality of regressive coenopopulations and the fact that most coenopopulations do not survive to this age.

# THE LARGE LIFE CYCLE OF A COENOPOPULATION

These selected species of grasses indicate the high diversity in coenopopulation age-state structure and population density that may be observed in nature. Each coenopopulation is in a particular stage of development at any specific moment and is marked by a 'specific age level' according to Uranov (1975). Uranov assumed that each age-state had a particular numerical value, reflecting its developmental status: the closer the individual came to completing its ontogeny, the larger its numerical value. Denoting the value of individuals in the *i*th age-state by  $m_i$  and the number of individuals in the same group by  $k_i$ , the 'coenopopulation age level' ( $\Delta$ ) was calculated as

$$\Delta = \frac{\sum k_i m_i}{\sum k_i}.$$

The higher this weighted mean, the older the population. The following values were assigned by Uranov (1975) to various age states:  $\mathbf{pl} = 0.0067$ ,  $\mathbf{j} = 0.018$ ,  $\mathbf{im} = 0.047$ ,  $\mathbf{v} = 0.119$ ,  $\mathbf{g}_1 = 0.27$ ,  $\mathbf{g}_2 = 0.50$ ,  $\mathbf{g}_3 = 0.731$ ,  $\mathbf{ss} = 0.880$ ,  $\mathbf{s} = 0.953$ .

In the course of development, the coenopopulation of any species is often subjected to unidirectional and irreversible changes in population density, age-state composition and productivity; that is, it is unstable and successive. The development may be reversible if a regressive coenopopulation is rejuvenated to the normal age-state spectrum; this may occur if ecological conditions change abruptly during succession.

Many meadow plants including grasses may be in a state of dynamic equilibrium with the habitat in one of the stages of their development: then the coenopopulation density and age-state composition undergo fluctuations only and the age-state structure remains relatively stable. According to Uranov and Smirnova (1969), those are the 'definitive coenopopulations'. The combination of reversible and irreversible changes in population density and age structure ensure cyclic coenopopulation development, accomplished by the multiple regular or (more frequently) irregular replication of reproduction waves throughout the large wave of the population flow. Only a single manifestation of the large wave is observed under extremely unfavourable conditions.

The full extent of a large coenopopulation wave can only be observed extremely rarely in natural phytocoenoses: in fact, it has not been previously described in literature for one and the same coenopopulation. Here we describe it for *Poa annua* (Fig. 2) in an establishing marginal meadow phytocoenosis in the Moscow region under conditions of intensive anthropogenic disturbance. In May the *Poa annua* coenopopulations



*Fig. 2.* Large wave of coenopopulation flux in (a) *Poa annua*, (b) *Deschampsia flexuosa*, (c) *Festuca pratensis*, (d) *D.caespitosa*. The duration of the wave varies: 5 months in *P.annua*, 4–6 years in *F.pratensis*, 20 years or more in *D.flexuosa* and 30–70 years in *D.caespitosa*. The relative percentage in each age-state group is shown on the ordinate.

were invasive with a high population density of 125–175 seedling and juvenile plants per  $0.25 \text{ m}^2$ . After two weeks some of these became immature and virginile and in mid-June about 30% of the individuals reached flowering stage ( $\mathbf{g}_1$  and  $\mathbf{g}_2$ ): the coenopopulation then passes into the young normal state. In early July the coenopopulations were maturenormal with a prevalent generative fraction,  $\mathbf{g}_2$  individuals constituting more than a half (55%). In late July and August old generative individuals were prevalent (45%) and the coenopopulations ageing; pregenerative plants were completely absent. Coenopopulation development was associated with a regular decrease in density and a gradual transfer of young individuals into the subsequent age-states. The large coenopopulation wave was essentially completed in September. No new reproduction wave was found in autumn. However a coenopopulation which included both the end of an old wave and the beginning of a new wave was described for an adjacent plot (Fig. 2a) in September 1981.

In the other species investigated only single stages of the large wave were observed. Nevertheless, essentially all stages of the large wave were traced in a spatio-temporal sequence of pasture degradation for *Deschampsia caespitosa* (Fig. 2). As already mentioned, the 1–2 year old cattle tracks and pastures are marked by the occurrence of invasive coenopopulations of this species and the 6–8, 15–30, 40 and 50 year old plots used for grazing are characterised by the young and mature, mature, ageing, old and temporarily regressive coenopopulations, respectively. The regular coenopopulation ageing was confirmed by studies of *Deschampsia* in the Oka flood-plain in 1960–1980. A mature coenopopulation on a 30-year old pasture turned into an ageing coenopopulation after seven years in the Oka meadows and an invasive coenopopulation reached a young normal state and then a mature normal state after 11 and 18–20 years, respectively.

This large wave is not highly localized, since similar stages in development of this species have been described for other parts of its range, in the north of the European part of the USSR and in Carpathian regions. It covers a period from 30 to 70 years.

A large coenopopulation wave of D. *flexuosa* was described for the meadowed felling areas (Fig. 2c). It covers a total period of 30–70 years. The old-normal coenopopulations occur in the 'definitive state' only in the forests, while the rest of the stages are successive.

In *Festuca pratensis* the large coenopopulation wave was traced in agrophytocoenoses and had a duration of 5–6 years (Fig. 2d). Therefore the absence of a number of coenopopulation age structure versions of this species in natural phytocoenoses seems to indicate the brevity of their existence and apparent instability, with the exception of the definitive ageing-normal and old-normal types. Numerous transitions of one of such coenopopulations of *Festuca pratensis* from the old normal state to the ageing state and vice versa, resulting from changes in the conditions of meadow uses and its intensity, are shown in Fig. 3a. The spectrum type



Fig. 3. Fluctuation variability of Festuca pratensis coenopopulation age-state spectra on flooded meadows: (a) frequent fluctuations, (b) rare fluctuations. Relative frequency of each age-state group (% of the total population density) is shown on the ordinate.

changed 5 times in 15 years. Fluctuational changes are as a rule less frequent, occurring after 5-6 and even 13 years (Fig. 3b). Such fluctuations are mainly caused by the changes in prevalence of the old generative and subsenile plants. The distribution of the roles of these two age-states depends on the death of their representatives and on the transition of individual plants from  $g_3$  to ss and vice versa, which occurs in cases of drastic environmental changes. The third and perhaps the principal cause of the changing roles of  $g_1$  and ss plants is the senile decay of the old generative and subsenile plants, resulting now and then in the prevalence of either the secondary generative particules or secondary subsenile particules. The fluctuating changes in Festuca pratensis spectra were less frequently caused by annual fluctuations in the young part of the coenopopulation. For example complete or nearly complete absence of seed replenishment for many years on hay meadows was followed by an extremely large reproduction wave, related to a strongly disturbed coenosis. The majority of the emerged young plants died, however, and the old normal coenopopulation was re-established (Fig. 3b).

According to Kurchenko (1974), the small wave lasts about 5 years in *Agrostis tenuis*, while in *Poa annua* the large wave may occur within 1-1.5 years. In both cases all coenopopulations of these species are successive and unstable.

Thus, the length of the large wave as a whole and the duration of the definitive coenopopulation in different grass species are different, and determined by the duration of individual ontogeny stages, reproductive periodicity, viable seed reserves and the intensity of vegetative reproduction by non-rejuvenated or rejuvenated particules. (A non-rejuvenated particule is a particule of the same age-state as the parent individual; the rejuvenated particule is a particule that has passed into an earlier age-state).

#### MODES OF SELF MAINTENANCE

The comparison of these species indicates not only their different rates of development, but also their different modes of coenopopulation self-maintenance.

*Poa annua* is marked by seed reproduction and a new generation develops in the same year as the parent individuals or in the following year: there is a rapid replacement of reproduction waves, lasting as long as the large wave. *Deschampsia caespitosa* and *Festuca pratensis* are also characterised by seed reproduction. However, because of their longer ontogeny, senile particulation to ensure retention of the species territory by non-rejuvenating vegetative progeny is essential. It is of particular importance if seed reproduction ceases: in *Deschampsia caespitosa* this process starts after 8–20 years, while in *Festuca pratensis* it starts after 7–13 years (but in agrocoenoses after 3–4 years). The age of each particule is also much larger in tussock-grass than in meadow fescue.

*D.flexuosa* is characterised both by seed and vegetative reproduction and the separating particules may either remain in  $g_3$  or ss or become rejuvenated to **j** or **im** age-state. Seed reproduction is prevalent in young, well-lit forest felling areas. Seed and vegetative reproduction is typical of the old felling areas overgrown with trees and bushes, but particule rejuvenescence does not occur in the initial stage. Seed reproduction is inhibited as the coenosis becomes saturated with edificator species, and then the separating individuals of vegetative origin become considerably rejuvenated (Zhukova 1979). Seed reproduction is absent in forest phytocoenoses in spite of the low species occurrence. The seedlings and drastically rejuvenated particules can only emerge in well-lit patches of the forest. Thus common hairgrass demonstrates one of the most stable coenopopulations.

In Agropyron repens on fallow and meadow agrophytocoenoses vegetative reproduction with rejuvenated or non-rejuvenated partial tufts is prevalent. Seed reproduction is essentially completely inhibited since no seedlings or other age-states of the young growth of seed origin were found in any of the coenopopulations described.

The concept of stable and unstable coenopopulations and of different intermediate versions (Rabotnov 1978) is based on their density dynamics and fluctuation ranges, and should be supplemented by concepts of coenopopulation age-state structure stability and lability. The stable coenopopulation must preserve the prevalence of certain groups of the adult population part. The rest of the age-state groups (primarily those belonging to the pregenerative period) are subjected to substantial fluctuation changes caused by periodicity of reproduction waves.

Coenopopulation life consists of alternating stable and unstable stages differing in duration and depending on the exogenous and endogenous factors. Among the exogenous abiotic factors affecting coenopopulation self-maintenance the most important are the weather and edaphic conditions and the mode and intensity of anthropogenic effects. The most influential exogenous biotic factors are the effects of other species of plants, animal and microorganisms, either by weakening the coenopopulation (by elimination of caryopses or vegetative organs or by diseases) or by contributing to its prosperity (mycorrhizal formation, the effects of biocoenotic microorganisms or zoocomponents, eradicating and decomposing the dead parts of grasses). Among the endogenous factors the most significant is saturation of the coenosis by the species itself. This is determined by indicators of the projective coverage, area of occupancy and phytomass, which depend on the density, vitality and age level of the coenopopulation. The higher the saturation, the weaker is rejuvenation in the coenopopulation, and vice versa. This is a regulative mechanism of self-maintenance. Simultaneously, it defines the actual role of the species in a real coenosis: potential edificators and dominants, for example, realise their possibilities most fully under high coenosis saturation.

The investigations done in different coenoses show that the dominance effect of various species depends on the development stage of a coenopopulation and not on habitat conditions. Sometimes the coenopopulation age level of dominant plants can determine phytocoenosis composition. For example, there may be decreasing diversity of species on different meadows during coenopopulation maturation, but a subsequent increase later as the coenopopulation ages.

#### CONCLUSIONS

1. The longevity of specific age-states determines the age level of the coenopopulation with the highest frequency in each species: for *Deschampsia caespitosa* these are the mature and ageing coenopopulations; for *D. flexuosa* and *Festuca pratensis* – the ageing and sensile coenopopulations; for *Poa annua* and *Agropyron repens* – all variants of normal coenopopulations.

2. The modes of self-maintenance of meadow grass coenopopulations depend on their ontogeny type and on their capacity for vegetative reproduction and rejuvenescence: their realisation is determined by the effect of exogenous abiotic and biotic factors and on the coenotic situation. The following coenopopulations can be distinguished on the meadows: those with seed reproduction alone, those with seed and vegetative reproduction and those with vegetative reproduction predominating.

3. The most stable species are able to change their self-maintenance modes in a strongly varying ecological situation, either by combining seed and vegetative reproduction or by alternating both types.

4. For coenopopulations of meadow grasses the basic ways of invading a territory in disturbed communities are (a) intensive seed reproduction from caryposes, stored in soil or dispersed from elsewhere, and (b) expansion of tussocks, rhizomes and stolons by intensive vegetative reproduction.

5. In meadow grasses, the principal way of holding occupied territory is by particulation of tussocks or of polycentric systems in long-rhizome and stolon-forming plants.

6. The species undergo selection in the meadows according to their labile responses to the rapidly changing environmental conditions. Rapidly developing coenopopulations are prevalent in meadow phytocoenoses.

7. The coenotic value of each species varies with the different development stages of coenopopulations. Maximum saturation of the habitat is realised by different variants of normal coenopopulations.

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