

Ewa SYMONIDES

Department of Plant Ecology, Institute of Botany, Warsaw University,
Al. Ujazdowskie 4, 00-478 Warsaw, Poland*

THE STRUCTURE AND POPULATION DYNAMICS OF PSAMMOPHYTES ON INLAND DUNES

II. LOOSE-SOD POPULATIONS

ABSTRACT: Population properties are presented of several plant species – dominants in psammophyte communities of low density, and changes in the specific composition and abundance structure of selected communities in the years 1968–1975. Communities with a coverage of 40–60% in the first study year were considered to be loose sods. The expansion of *Tragopogon heterospermus* Schweigg. and *Carex arenaria* L. was found to cause a considerable transformation of the phytocenotic relations of psammophyte communities. The two species have shown a great dynamism and competitive power. Populations of the following species have shown a relatively low sensitivity to the competitive action of *T. heterospermus*: *Koeleria glauca* (Schkuhr) DC. and *Festuca psammophila* (Hackel) Krajina. Irregular variations in the specific composition and population abundance of individual components were found in a patch of the association *Corispermo-Plantaginetum indicae*.

KEY WORDS: Inland dunes, psammophytes, succession, polycormones, survival curves, age composition, loose-sod populations, dynamics of phytocenoses, reproductiveness, mortality.

Contents

1. Introduction
2. Results
 - 2.1. Changes in the vegetation of a *Spergulo-Coryneporetum* patch due to the encroachment and retreat of *Carex arenaria* population
 - 2.2. The dynamics and succession of sods of the association *Festuco-Koelerietum glaucae*
 - 2.3. Population properties of species dominating in the association *Festuco-Koelerietum glaucae*
 - 2.3.1. *Koeleria glauca*
 - 2.3.2. *Festuca psammophila*
 - 2.3.3. *Tragopogon heterospermus*
 - 2.3.4. *Androsace septentrionalis*
 - 2.4. The dynamics of semisynanthropic dune communities as exemplified by *Corispermo-Plantaginetum indicae*

*Correspondence address: Akermanńska 5 m. 37, 02-760 Warsaw, Poland.

- 2.5. Populational and individual variation of *Plantago indica*
3. Discussion
4. Summary
5. Polish summary
6. References

1. INTRODUCTION

The present study is part of a series of wider-scope investigations concerned with the ecology of selected plant species and psammophyte communities. The aims of the studies were: (1) to follow changes in the structure and role of the populations of individual species in the formation and succession of plant communities; (2) to analyse the course and rate of inland dune overgrowth.

The investigations were carried out in the Toruń Basin between March 1968 and July 1975. The study area included ten permanent sites representing various phases of dune overgrowth; a description of the soils, climate and vegetation of the study area can be found in the paper by Symonides (1974).

In the first paper (Symonides 1979a) the course is described of bare sand colonization (sites 1 and 2), the development of the initial patch of the Spergulo-Corynephoretum (Tx. 1928) Libb. 1933 (site 3), and the structure and dynamics of three *Corynephorus canescens* (L.) P. B. populations. Because of its pioneer role, *C. canescens* has been given much attention.

The present, the second part of the study contains the most important results from studies carried out on loose psammophyte sods, the "loose sods" being plant communities with a coverage of 40–60% in the first study year. The patches selected for study represented the following plant associations: Spergulo-Corynephoretum in its optimum growth phase (site 4), a community with *Carex arenaria* (site 5), Festuco-Koelerietum glaucae Klika 1931, a facies with *Androsace septentrionalis* L. (site 6), Festuco-Koelerietum glaucae, a typical variant (site 7), and Corispermo-Plantaginetum indicae Passarge 1957 (site 8). The inner dynamics and succession of the above-enumerated communities were analysed over a period of several years on the basis of changes in the specific composition and numbers, cover, frequency and biomass of the populations of the particular component species. Subjects to a wider-scope research were the populations of plants characteristic of the associations and at the same time dominant in the selected patches: *Carex arenaria* — on sites 4 and 5, *Koeleria glauca* and *Festuca psammophila* — on sites 6 and 7, *Androsace septentrionalis* and *Tragopogon heterospermus* — on site 6, and *Plantago indica* L. — on site 8. For the populations of these species an assessment was made of the seasonal and many-years' variations in density, spatial structure, age and size structure, in reproductiveness, mortality, and net increase and production of biomass.

For the population studies, in each of the sites (256 or 100 m² in surface area) four plots, each of 4 m², were set out for *F. psammophila* and *T. heterospermus*, and 1 m² — for the remaining plant species. In addition to the permanent observation plots, for the populations of *C. arenaria* and *P. indica* each year data were taken into account from all the plots at the sites where there occurred at least one individual; in the case of *P. indica* it was necessary to increase the size of the sample, because of a great variation in population abundance and density in both time and space; in case of *C. arenaria* — because of the specific way of polycormone growth. All *C. arenaria* shoots found on sites 4 and 5 in 1968, at the beginning of the study, were charted. The cartogram was regularly completed over the several study years as individuals appeared and

disappeared. Flowering, fruiting and dying shoots were marked with appropriate symbols. The cartogram provided the basis for statistical analyses of the results.

A map showing the location of the study sites, and a detailed description of the methods can be found in the first part of the study (S y m o n i d e s 1979a).

2. RESULTS

2.1. CHANGES IN THE VEGETATION OF A SPERGULO-CORYNEPHORETUM PATCH DUE TO THE ENCRoACHMENT AND RETREAT OF *CAREX ARENARIA* POPULATION

Although the psammophyte communities with *Carex arenaria* occupy relatively small parts of the dunes under study, they stamp them specifically with the characteristic physiognomy of the sedge sod. *C. arenaria* shoots, put out in regular rows by interlacing runners pointed in different directions, form a sort of network with bare sand showing through the meshes, or individuals of other psammophyte species growing in the open spaces. *C. arenaria* shoots always grow only on one end of a polycormone and they die on the opposite side, for this reason a sedge sod "travels" until it encounters an obstacle in the form of a too dense growth of grassy vegetation.

To follow changes in the qualitative and quantitative composition of the communities due to the encroachment and retreat of a sedge population, and to analyse the rate and the mechanisms of the "travelling" of a sedge sod, two observation sites were selected. One of them (4) was located at the edge of a young part of a small sod so that it contained primarily the propagating ends of the polycormones. The vegetation of this site represented a floristically rich, well-developed patch of Spergulo-Corynephorum, consisting of 23 plant species jointly covering 40% of the area; 30.2% of the total number of individuals of flowering plants was represented by *C. arenaria* shoots concentrated over 1/3 of the area.

The retreat of a sedge population was studied in a different sod which was compact, dense and with a high percentage of old shoots; in this case the site concerned (5) was crossed by an edge of dying sod. The sedge shoots occupied 2/3 of the surface area and represented 98.2% of the total number of plants in the community. The remaining few plants belonged to three grassy species: *Koeleria glauca*, *Festuca psammophila* and *F. duriuscula* L. Grass tussocks occurred almost exclusively in areas deserted by dying sedge shoots. In 1968, the total cover at this site amounted to about 50%.

Table I contains a summarized description of more important indices of the structure, reproductiveness, mortality and biomass of both *C. arenaria* populations during the study period. Figures 1 and 2 illustrate the growth and the dying of a population, as exemplified by one plot from each site.

In the progressive population (site 4) there was a more than five-fold increase in the number of individuals; only 62.3% of the new shoots were produced by those polycormones that were present at the site already in the first study year; the remaining shoots appeared as a result of the propagation of the polycormones that penetrated each year from outside the site; the number of polycormones doubled.

As a result of the penetration and formation of new shoots, there was a continual increase in frequency and population density. At the end of the eight years' period the travelling "head" of the population appeared to have moved forward over a distance of 3.2–4.4 m, thus the total surface area colonized by *Carex* had increased by 32% (Fig. 3).

Table I. Indices of structure, reproductiveness, mortality and biomass production in *Carex areanaria* populations on sites 4 and 5
 1 - number of polycormones in the area (100 m²), 2 - total number of shoots in the area, 3 - density per 1 m², 4 - frequency (%), 5 - proportion of juveniles (%), 6 - proportion of senile individuals (%), 7 - reproductiveness: number of new individuals per 1 polycormone, 8 - average number of dead individuals per 1 polycormone, 9 - total mortality of the population (%), 10 - biomass production (kg d. wt), 11 - diaspore production (in thousands), a - progressive population (site 4), b - regressive population (site 5)

Year	Indices																			
	1		2		3		4		5		6		7	8	9		10		11	
	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b
1968	75	269	507	4944	14.4	69.9	35	71	38.8	0.95	0	16.2	2.86	1.70	0	2.2	0.26	1.87	23.9	311.5
1969	95	261	749	4881	20.2	68.8	37	71	32.3	0.32	0	29.5	2.72	2.29	0	2.7	0.38	1.70	39.2	284.5
1970	109	249	1047	4424	26.8	68.0	39	65	28.5	0.15	0	22.3	2.85	5.54	0.19	31.0	0.52	1.61	57.9	270.9
1971	111	211	1237	3050	30.2	57.5	41	53	15.4	0	0	27.0	2.68	0.44	0.65	3.0	0.57	1.08	80.9	181.3
1972	120	209	1481	2958	31.5	56.9	47	52	16.5	0	0.81	32.9	3.20	1.50	1.69	9.8	0.68	1.01	95.4	169.1
1973	139	192	1757	2669	33.8	56.8	52	47	15.7	0	2.2	49.9	2.76	2.38	2.67	17.0	0.81	0.81	113.5	134.0
1974	168	173	2183	2216	37.0	54.0	59	41	19.5	0	3.5	69.3	3.30	6.30	2.88	27.7	1.03	0.59	132.8	95.2
1975	174	102	2550	1126	38.1	37.5	67	30	14.4	0	9.8	82.2	2.70	3.12	2.94	27.7	1.16	0.27	162.6	42.7

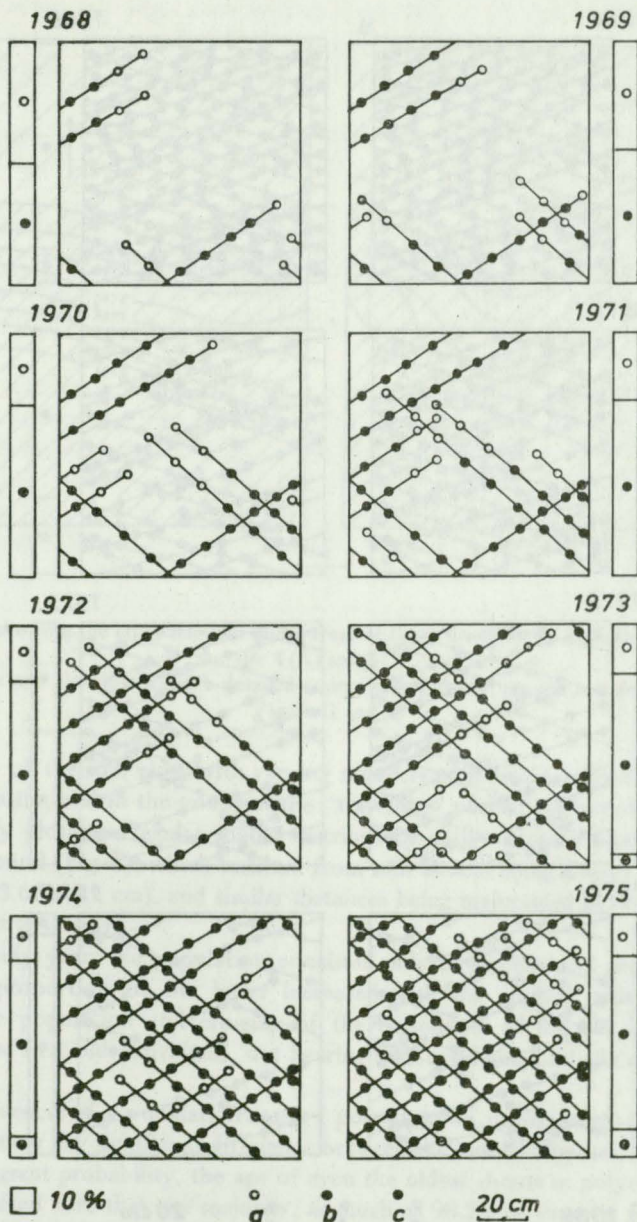


Fig. 1. Overgrowing of a plot by *Carex arenaria*, and the proportions of shoots in different growth stages in a progressive population (site 4)

Types of shoot: a - this year's, young, b - flowering and fruiting, c - non-fruiting, old. Height of column (100%) - total number of shoots on site; the lines connect individuals of the particular polycormones

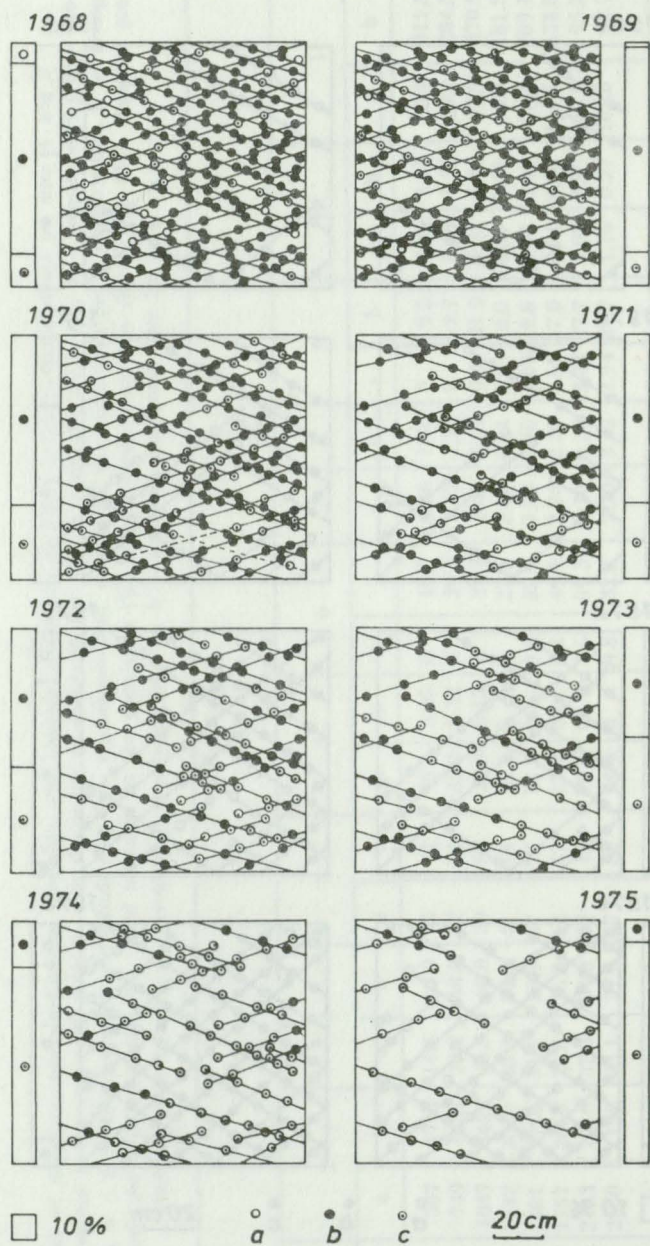


Fig. 2. Dying of shoots and decline of polycormones in a regressive population of *Carex arenaria*, as exemplified by a plot at site 5
 Explanations as for Figure 1

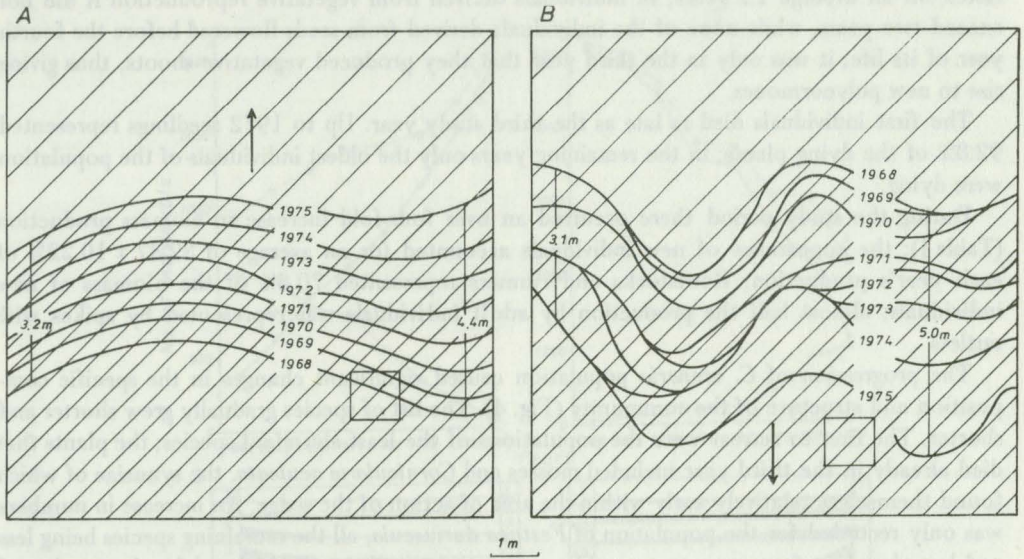


Fig. 3. A diagram showing the encroachment and retreat of *Carex arenaria* sod in individual study years on site 4 (A) and 5 (B). Marked on the site are plots for which a detailed course of population growth and decline is presented in Figures 1 and 2.

In older parts of the sod, plots with varying numbers of individuals formed a zone with a clearly higher density, and in the younger, the "travelling" part of the population – a zone of thinning. In many plots the regular spatial distribution, rare in natural plant populations, of individuals was found (Fig. 1), which resulted from new shoots being always sent up at similar intervals (every 13.65 ± 1.1 cm), and similar distances being maintained between rows of polycormones (11.85 ± 2.41 cm).

In the first study year, the population consisted only of juvenile and generatively mature individuals; the proportion of the latter increased with the gradual increase in the total abundance of the population and crossing of the boundaries of the site by the individual polycormones. The first old individuals, not bearing fruit and being partially dead, appeared as late as 1972.

The reproductiveness of a population as per 1 polycormone, propagating vegetatively within the site, did not show any significant difference between the individual years, so it was possible to estimate, with great probability, the age of even the oldest shoots in polycormone rows. It should be emphasized here that the majority, as much as 98.2% of the new individuals during the eight years' study period originated from vegetative propagation. Only 37 new individuals arose from seeds, and only 7 of them gave rise to new polycormones; the remaining individuals died after 3–4 months. Thus the efficiency of generative reproduction was low, especially when the high rate of diaspore production is taken into account (Table I). An average fructifying individual produced 77.38 ± 13.7 diaspores a year for 5–9 years.

Most of the generative shoots flowered and produced fruit throughout the eight consecutive years. The flowering shoots always attained a similar height of 12.7 ± 1.1 cm, insignificantly

varying from year to year and from plot to plot. On site 4, the juvenile phase of *C. arenaria* lasted on an average 1.2 years; in individuals derived from vegetative reproduction it did not exceed two years, while none of the individuals derived from seeds flowered before the fourth year of its life; it was only in the third year that they produced vegetative shoots, thus giving rise to new polycormones.

The first individuals died as late as the third study year. Up to 1972 seedlings represented 92.8% of the dying plants; in the remaining years only the oldest individuals of the population were dying.

During the study period there occurred an over four-fold increase in biomass production (Table I); the appearance of new individuals accounted for an average of $32.37 \pm 10.22\%$ of each year's production. Rootstocks and runners represented 70.8% of the biomass of new individuals; almost half the production by adult individuals was represented by spikes with nutlets.

The progression of *C. arenaria* population caused significant changes in the specific composition and structure of the community (Fig. 4). The list of species gradually grew shorter and shorter. The first to retreat were the populations of the least abundant species; the plants that died already in the third year included mosses and *Cornicularia aculeata*, the synusiae of which found themselves relatively early within the area of action of the sedge. An increase in numbers was only recorded for the population of *Festuca duriuscula*, all the remaining species being less and less abundant from year to year. The correlation coefficient, calculated for the number of individuals of *C. arenaria* and total number of individuals of the remainder² of species ($r = -0.988$), indicated a close, statistically significant even at 1% level of error risk, negative correlation between the increase in numbers of *C. arenaria* and the abundance of the populations of the species co-occurring with it in the study area. Except for a few tussocks of *F. duriuscula* and *F. psammophila*, the surviving plants occurred only in the part of the area so far not occupied by the sedge sod.

Corynephorus canescens appeared to be competitively weak; because of the lack of new growth, only 16 (out of the original 251) old non-flowering tussocks lasted until the end of the studies.

The increase in the total number of individuals in the study area (Fig. 4) resulted primarily from a dynamic growth of the *C. arenaria* population whose shoots represented in the last year 94.5% of the total number of individuals in the community. Because of the small cover provided by the sedge shoots, and the retreating of the cryptogamous plants, there occurred a considerable decrease (down to 20%) in the overall coverage of the sand area, although as a result of the even spatial distribution of *C. arenaria* shoots, the sands had been more successfully fixed.

During the study period there occurred a slight increase in the total biomass of the community: from 2.82 kg in 1968 to 3.16 kg in 1975; in the last study year the contribution of *C. arenaria* constituted 64.07% of the total biomass.

As a result of the dying of the oldest parts of *C. arenaria* polycormones, the boundaries of the "regression" of the sedge sod from site 5 were found to have moved during the study period by a distance of 3.1–5.0 m (Fig. 3), whereas the total number of individuals in the population was found to have decreased more than four times. The rate of the retreating of the population from site 5 was similar to the rate of encroachment of the population on site 4. However, although the average number of new individuals produced by the individual polycormones in the consecutive years was very similar (2.88 ± 0.23), the number of dying individuals clearly differed (Table I). This resulted in a jumping, uneven decrease in population abundance, and a movement of the sod boundary, uneven at the different points of the site (Figs. 3, 4).

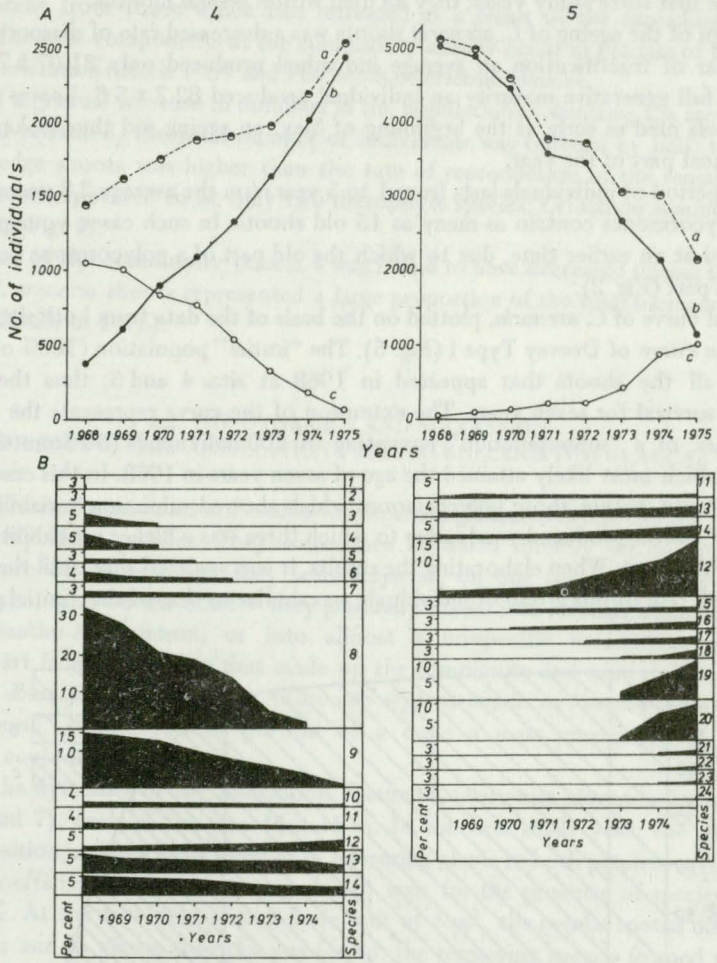


Fig. 4. Changes in the specific composition and structure of a community, as a result of the encroachment (site 4) and retreat (site 5) of *Carex arenaria* population

A – total number of plants on the site (a), number of *C. arenaria* shoots (b), and the number of individuals of other species (c); B – specific composition and quantitative relations among the populations of species accompanying the sedge; 100% – total number of plants on the site. Species: 1 – *Carex hirta* L., 2 – *Scleranthus perennis* L., 3 – *Plantago indica*, 4 – *Veronica dillenii* Cr., 5 – *Sedum sexangulare* L., 6 – *Helichrysum arenarium* (L.) Moench, 7 – *Jasione montana* L., 8 – *Spergula vernalis* Willd., 9 – *Corynephorus canescens* (L.) P. B., 10 – *Potentilla arenaria* Borkh., 11 – *Thymus serpyllum* L., 12 – *Festuca duriuscula* L., 13 – *Koeleria glauca*, 14 – *Festuca psammophila*, 15 – *Artemisia campestris* L., 16 – *Centaurea rhenana* Bor., 17 – *Armeria elongata* (Hoffm.) Koch, 18 – *Veronica spicata* L., 19 – *Cerastium semidecandrum* L., 20 – *Erophila verna* (L.) C. A. M., 21 – *Hernaria glabra* L., 22 – *Dianthus carthusianorum* L., 23 – *Potentilla argentea* L., 24 – *Dianthus deltoides* L. In addition to the above-listed, the following were represented by single individuals on site 4: *Rumex acetosella* L., *Euphorbia cyparissias* L., *Trifolium arvense* L., *Centaurea jacea* L., *Peucedanum oreoselinum* (L.) Moench and *Pinus sylvestris* juv. L. (a total of 10 individuals), and *Polytrichum piliferum* Schreb., *Rhacomitrium canescens* L. and *Cornicularia aculeata* (Schreb.) Ach., covering a total of about 1.5 m² surface area

New polycormones and individuals appeared in this population only in small numbers and only during the first three study years; they all died within several months.

The first sign of the ageing of *C. arenaria* shoots was a decreased rate of diaspore production. In the last year of fructification an average individual produced only 31.07 ± 7.2 diaspores, whereas in its full generative maturity an individual produced 82.7 ± 5.3 . Leaves and stems of senile individuals died as early as the beginning of May; an ageing sod thus looked completely dead for the most part of the year.

The senile period of individuals lasts from 1 to 5 years (on the average 2.8 years). Because of this, some polycormones contain as many as 15 old shoots. In such cases, younger individuals sometimes died at an earlier time, due to which the old part of a polycormone became cut off from the main part (Fig. 2).

The survival curve of *C. arenaria*, plotted on the basis of the data from both sites, is a typical example of the curve of Deevey Type I (Fig. 5). The "initial" population (100% of individuals) consisted of all the shoots that appeared in 1968 at sites 4 and 5; thus the curve truly represents its survival for seven years. The extension of the curve represents the dying, in the successive years, of a "subpopulation" consisting of 200 individuals (80 from site 4 and 120 from site 5), which most likely attained the age of seven years in 1968. In this case shoots were taken into account within those polycormones which showed minimum variability as regards the number of shoots produced yearly, due to which there was a higher probability of a correct assessment of their age. When elaborating the results, it was assumed that until the seventh year of life the death rate of this group of individuals was similar to that of the "initial group".

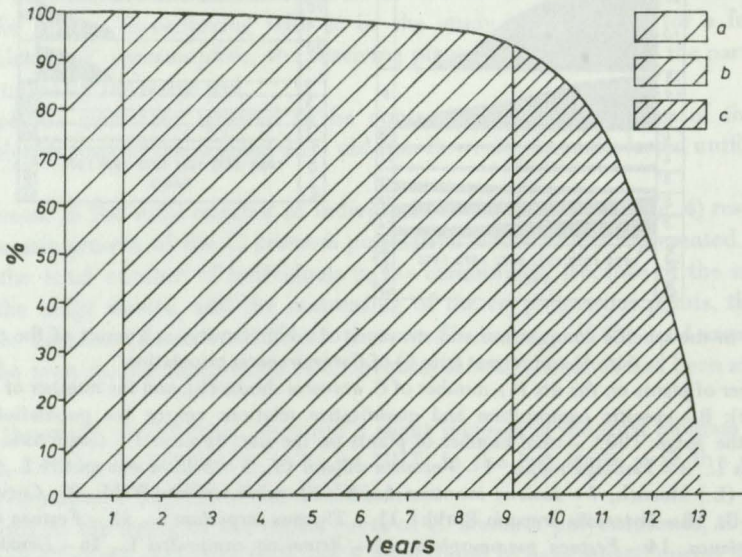


Fig. 5. An approximate curve of survival of *Carex arenaria* population and the duration of each life period a – juvenile period, b – period of generative maturity, c – senile period

Due to the changes in the age structure of the regressive population, the production of organic matter fell much faster than the number of individuals. At the end of the research it was 7.01 times lower than in 1968, while the level of numbers was 4.39 times lower (Table 1).

Places left by the dying sedge shoots were gradually colonized by populations of other psammophytes; the floristic list of the community was increased by a total of 10 new species (Fig. 4) different from those which had retreated as a result of the spreading of the sedge population. The new components of the community usually occur in patches of the association *Diantho-Armerietum* Krausch 1959 and *Festuco-Koelerietum glaucae*.

In spite of a gradual increase in numbers in the populations colonizing the areas from where the sedge had retreated, the total number of individuals was reduced by half; thus the dying rate of the sedge shoots was higher than the rate of reproduction of the remainder of plant species. Numerous appeared to be only two therophyte species: *Cerastium semidecandrum* and *Erophila verna* (Fig. 4).

The biomass of the community on site 4 was found to have decreased during the eight years by 1.37 kg; *C. arenaria* shoots represented a large proportion of the total biomass until the end of the study (28.2% in 1975).

2.2. THE DYNAMICS AND SUCCESSION OF SODS OF THE ASSOCIATION *FESTUCO-KOELERIETUM GLAUCAE*

In the study area the association *Festuco-Koelerietum glaucae* was represented by numerous, though not very large patches. They sometimes bordered directly on an area with bare, quick-sand, more often, however, they were adjacent on one side to patches of *Spergulo-Corynephorum*, and on the other — they gradually passed into strongly compact sods of the association *Diantho-Armerietum*, or into almost a unispecific community with *Festuca duriuscula*. Apart from the grasses that made up the community and were characteristic of the association, in some patches abundant *Androsace septentrionalis* or *Festuca duriuscula* populations were found. In the eastern portion of a dune a mass emergence of *Tragopogon heterospermus* could be seen.

Studies of the dynamics of the association *Festuco-Koelerietum glaucae* were carried out at two sites (6 and 7), each of the size 16 × 16 m. In the first study year, the physiognomy, specific composition, and the total number of flowering plants in both patches were similar; the "community coefficient" (Ellenberg 1956) was: for the presence of species 90.5%, for abundance 75%. At the two sites, with a basic unit of 4 m², the regular spatial distribution of *F. psammophila* and *K. glauca* tussocks was found; the remaining species formed more or less visible aggregations. In the first study year the sites differed primarily in the growth of vegetation, composition and numbers of the dominants, and in the abundance relations between the remaining components of both communities (Tables II, III); the dominant populations were identified on the basis of the proportion of their individuals in the total number of plants. This proportion was assumed to exceed 10%.

The direction and rate of changes in the vegetation, different at each site (Tables II, III) resulted in a decrease in the overall floristic similarity down to 29.4%, and a slight increase in the community coefficient for abundance — up to 78.4%. A common feature of the dynamics of the communities was an increase in coverage (up to 100%) and a reduced list of species.

The most important changes at site 6 were the following:

1. A rapid expansion of *Tragopogon heterospermus* population. Whereas in 1968 the population was the least abundant, the following year it already belonged to the dominant group of the community, and two years later it dominated numerically over the populations of other dominant species, while in the last study year the individuals of this population

Table II. Specific composition and population numbers in a patch of *Festuco-Koelerietum glaucae* (site 6)
 Syntaxonomic units have been identified according to Krausch (1968)

Species*	1968	1969	1970	1971	1972	1973	1974	1975
Character-taxa <i>Koelerion glaucae</i>								
<i>Koeleria glauca</i>	3392	3658	3184	3449	2932	2228	1827	1699
<i>Festuca psammophila</i>	3825	3824	3520	3820	3362	2992	2492	2326
<i>Androsace septentrionalis</i>	3720	3936	3260	3192	2876	2548	1636	347
<i>Gypsophila fastigiata</i> L.	36	2	2	0	0	0	0	0
<i>Plantago indica</i>	306	128	29	0	0	0	0	0
<i>Tragopogon heterospermus</i>	5	3381	4784	5671	6686	7360	7616	7928
Character-taxa <i>Armerion elongatae</i>								
<i>Armeria elongata</i>	11	9	6	4	0	0	0	0
Character-taxa <i>Corynephorion</i>								
<i>Corynephorus canescens</i>	312	276	208	74	27	0	0	0
Character-taxa <i>Festuco-Sedetalia</i>								
<i>Helichrysum arenarium</i>	278	267	136	47	19	7	0	0
<i>Thymus serpyllum</i>	49	36	32	11	9	2	0	0
<i>Cerastium semidecandrum</i>	96	1115	0	0	0	0	0	0
<i>Sedum reflexum</i> L.	830	625	221	0	0	0	0	0
Character-taxa <i>Sedo-Scleranthetea</i>								
<i>Arenaria serpyllifolia</i> L.	111	1127	0	0	0	0	0	0
<i>Hieracium pilosella</i> L.	308	149	107	47	21	11	0	0
<i>Jasione montana</i>	21	12	0	0	0	0	0	0
<i>Rumex acetosella</i>	36	31	25	13	0	0	0	0
<i>Scleranthus perennis</i>	42	38	31	17	0	0	0	0
<i>Trifolium arvense</i>	147	96	16	0	0	0	0	0
<i>Veronica dillenii</i>	211	925	0	0	0	0	0	0
<i>Festuca duriuscula</i>	217	236	257	278	318	496	656	1638
Character-taxa <i>Festuco-Brometea</i>								
<i>Artemisia campestris</i>	6	5	5	5	6	6	6	6
<i>Centaurea rhenana</i>	7	7	6	4	0	0	0	0
<i>Dianthus carthusianorum</i>	36	32	26	16	0	0	0	0
<i>Potentilla arenaria</i>	37	35	32	21	11	7	0	0
<i>Veronica spicata</i>	11	11	8	0	0	0	0	0
Other taxa								
<i>Pinus sylvestris</i> juv.	5	7	4	4	4	4	4	4
Total of individuals	14055	19968	15899	16673	16271	15661	14237	13948

*The lichen layer consisted of: *Cornicularia aculeata*, *Cetraria islandica* (L.) Ach., *Cladonia silvatica* (L.) Harm., *C. uncialis* (L.) Web. and *C. mitis* Sandst., with a joint coverage of 5–6 m² throughout the study period.

constituted 56.8% of the total number of flowering plants (Table II, Fig. 6 C). It should be mentioned that in the estimation of the numbers of plants in large areas seedlings were omitted, and their number in the case of *T. heterospermus* was (according to an approximate assessment on the basis of frequency and number of seedlings in the study plots) several dozen thousand. An immediate result of the dynamic growth of the population of *T. heterospermus* was the completion of the coverage of the surface, and the enrichment of the community with a new layer, the highest vegetation layer, already in the second study year, and a more than double increase in the biomass during the study period: from 46.42 to 110.81 kg per 256 m².

Table III. Specific composition and population numbers in a patch of *Festuco-Koelerietum glaucae* (site 7)
 Syntaxonomic units have been identified according to Krausch (1968)

Species*	1968	1969	1970	1971	1972	1973	1974	1975
Character-taxa Koelerion glaucae								
<i>Koeleria glauca</i>	3578	3570	3521	3519	3507	3486	3456	3434
<i>Festuca psammophila</i>	3486	3457	3398	3362	3308	3266	3237	3207
<i>Gypsophila fastigiata</i>	11	0	0	0	0	0	0	0
<i>Plantago indica</i>	212	174	168	196	175	213	142	274
<i>Tragopogon heterospermus</i>	1	147	162	211	272	325	348	511
Character-taxa Armerion elongatae								
<i>Armeria elongata</i>	98	102	136	139	151	163	165	177
Character-taxa Corynephorion								
<i>Corynephorus canescens</i>	174	98	11	0	0	0	0	0
Character-taxa Festuco-Sedetalia								
<i>Helichrysum arenarium</i>	176	172	161	156	150	131	119	96
<i>Thymus serpyllum</i>	516	516	518	518	521	521	521	523
<i>Cerastium semidecandrum</i>	318	121	276	408	516	621	427	530
<i>Sedum reflexum</i>	279	166	108	0	0	0	0	0
Character-taxa Sedo-Scleranthetea								
<i>Arenaria serpyllifolia</i>	168	156	78	0	0	0	0	0
<i>Hieracium pilosella</i>	307	147	62	21	0	0	0	0
<i>Jasione montana</i>	386	392	392	411	416	416	425	427
<i>Rumex acetosella</i>	78	96	54	50	21	0	0	0
<i>Scleranthus perennis</i>	77	70	65	47	11	0	0	0
<i>Trifolium arvense</i>	76	28	13	0	0	0	0	0
<i>Festuca duriuscula</i>	2766	2936	3247	3352	3419	3478	3512	3607
Character-taxa Festuco-Brometea								
<i>Artemisia campestris</i>	39	39	41	42	42	41	42	52
<i>Centaurea rhenana</i>	76	82	91	107	107	109	114	126
<i>Dianthus carthusianorum</i>	147	157	171	188	211	236	242	376
<i>Euphorbia cyparissias</i>	39	17	0	0	0	0	0	0
<i>Potentilla arenaria</i>	256	256	256	247	242	239	231	220
<i>Veronica spicata</i>	96	110	120	108	117	136	121	246
Total of individuals	13360	13009	13049	13082	13186	13381	13102	13806

*The lichen layer consisted of: *Cornicularia aculeata*, *Cetraria islandica*, *Cladonia silvatica*, with a joint coverage of 3–4.5 m² throughout the study period.

2. Almost four-fold reduction of the number of species in the patch (Fig. 6 A); the list of retreating plants included only flowering plants (Table II), the early-spring ephemerals being the first to die: *Cerastium semidecandrum*, *Veronica dillenii* and *Arenaria serpyllifolia*. The floristic similarity of the community in the first and the last study years was as low as 40.6%.

3. Considerable variations in the total abundance of plants at a site during the study period (Fig. 6 B); in 1975, the level of numbers of the plants approached the total abundance of individuals in 1968 (Table II).

4. A considerable, over ten-fold decrease in numbers in the *Androsace septentrionalis* population which was dominant in the first study year. In 1975 individuals of this species represented only 2.6% of the total number of flowering plants.

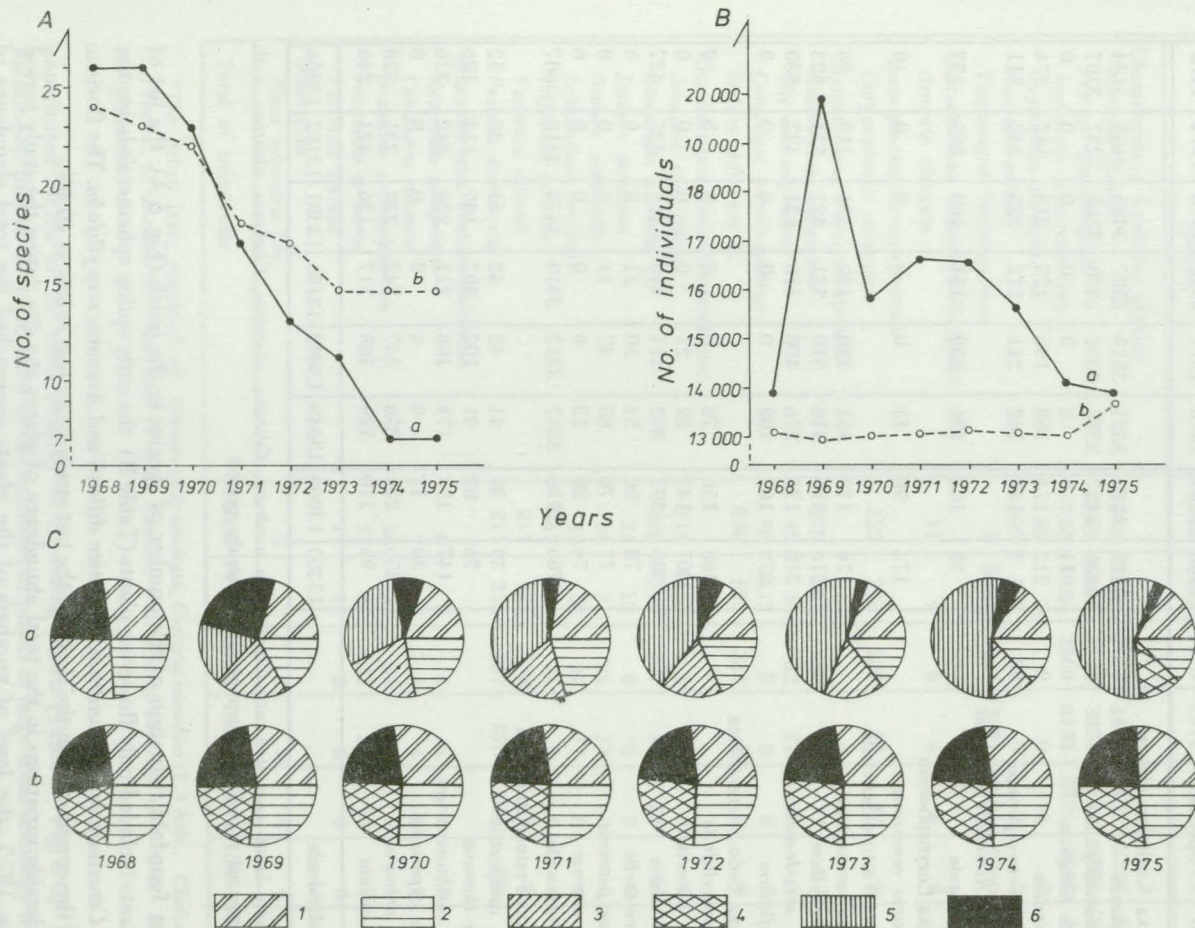


Fig. 6. Variations in the number of species (A), individuals (B), and in the abundance ratios between populations of different species (C) in Festuco-Koelerietum glaucae patches on site 6 (a) and 7 (b)

1 - *Koeleria glauca*, 2 - *Festuca psammophila*, 3 - *Androsace septentrionalis*, 4 - *Festuca duriuscula*, 5 - *Tragopogon heterospermus*, 6 - all other species jointly (cf. Tables II, III)

5. A decrease in numbers in the populations of *Koeleria glauca* and *Festuca psammophila*, down to 50.1 and 60.8%, respectively, of the level found in 1968.

6. A gradual increase in numbers of the *Festuca duriuscula* population which, in accordance with the criteria adopted, in the last study year found itself on the dominant list (Fig. 6 C, Table II). To study the course of the changes in the floristic composition of the patch in the successive study years, similarity indices were calculated according to the modified formula of Jaccard-Steinhaus (Whittaker 1973), commonly accepted by the followers of the Polish school of Wrocław Taxonomy. The distribution of the coefficients (Fig. 7) indicates that in the first study year the changes occurred rapidly, whereas in the following years steady gradual changes occurred, and it was only in the last year that a distinct difference occurred relative to the preceding year.

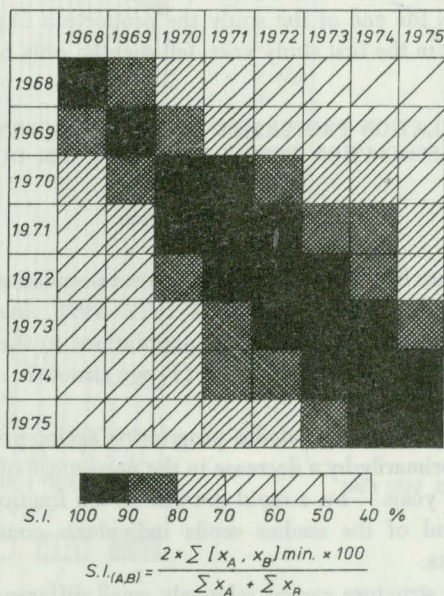


Fig. 7. Similarity index for the floristic composition of Festuco-Koelerietum glaucae patch (site 6) in consecutive years from 1968 to 1975

Similarity index (S. I.) – calculated according to the modified formula of Jaccard-Steinhaus (Whittaker 1973)

Much slower were the changes in the vegetation on site 7 (Table III, Fig. 6); at the end of the eight years the community coefficient for the presence of species was 70.0%, for abundance – 91.45%. The list of species became gradually poorer and poorer from year to year (Fig. 6 A), but because of the small size of the plants of most of the retreating species (*Arenaria serpyllifolia*, *Sedum reflexum*, *Trifolium arvense*, *Hieracium pilosella*), or their low numbers in the first study year (*Gypsophila fastigiata*, *Euphorbia cyparissias*), the changes were at first sight inconspicuous.

As a result of the slow increase in numbers of some species and at the same time a decrease in numbers of others (Table III), the total number of plants at site 7 slightly varied from year to

year (Fig. 6 B). Grasses dominated throughout the study period, their tussocks always representing about 3/4 of all the plants of the community.

A detailed analysis of the density of the grass populations, dominant at site 7 has revealed a slight tendency to decrease the abundance in the populations of *K. glauca* and *F. psammophila* (the average density was statistically insignificantly different). A clearer increase could be seen in the number of *F. duriuscula* tussocks; in the last study year their number was 1.3 times greater than in 1968. Much less intensive than at site 6 was the increase in numbers of *T. heterospermus*; in the last year they represented only 3.7% of all the plants at site 7, and 21.05% of total biomass. It must be pointed that adjacent to this site were experimental plots from which only half the total number of grass tussocks were removed in 1972. The following year *T. heterospermus* seedlings occurred in them in large numbers, as they did at site 6, and two years later there occurred a rapid increase in the number of flowering individuals.

The level of the plant biomass of the community at site 7 was found to have increased from 75.29 to 81.88 kg. Towards the end of the study the proportion of grasses, which constituted 75.29% of the total biomass in the first study year, fell slightly, only by 3.95%.

2.3. POPULATION PROPERTIES OF SPECIES DOMINATING IN THE ASSOCIATION FESTUCO-KOELERIETUM GLAUCAE

2.3.1. *Koeleria glauca*

Site 6. The main feature of the dynamics of *K. glauca* population was a steady decrease in the number of tussocks, especially in the years 1972–1975. Investigations performed in permanent plots revealed further reactions of the populations to the phytocenotic changes in the community. Noteworthy are two phenomena: (1) age structure changes and (2) changes in the manner of reproduction.

The population age composition indicated a progressing ageing process. It was evidenced – in the first study years – primarily by a decrease in the percentage of the youngest individuals, and during the subsequent years – by a rapid growth of the fraction of older dying tussocks (Fig. 8 A). Towards the end of the studies senile individuals constituted 67% of the total number of *K. glauca* tussocks.

Clear changes in the age structure caused relatively small differences in the contribution of the individuals of each group to the annual biomass production (Fig. 8 B). Generatively mature tussocks produced 59.5–76.1% of the biomass each year; the contribution of the senile individuals amounted to as little as several per cent, and it only slightly increased in the last study years. The increasing predominance of old tussocks in a population to some extent caused a lowering of the total yearly production of biomass.

The varying weather conditions in the particular study years (cf. Fig. 2 – Symonides 1979a) did not significantly affect the individual production of the tussocks of the same age group; very young and very old individuals always produced the least biomass, while juveniles (from the second year of life to the first flowering in the 4–5 year) produced several times more, tussocks 4–8 years old, that is, fully mature generatively, producing the most. For this reason, in 1972 when a fairly numerous group of individuals that developed in 1969 attained maximum productive potential, there occurred a rapid growth of the total biomass production, while in 1974 – as a result of the “becoming old” of a large number of tussocks – a nearly two-fold decrease relative to the preceding year (Fig. 8 A, C).

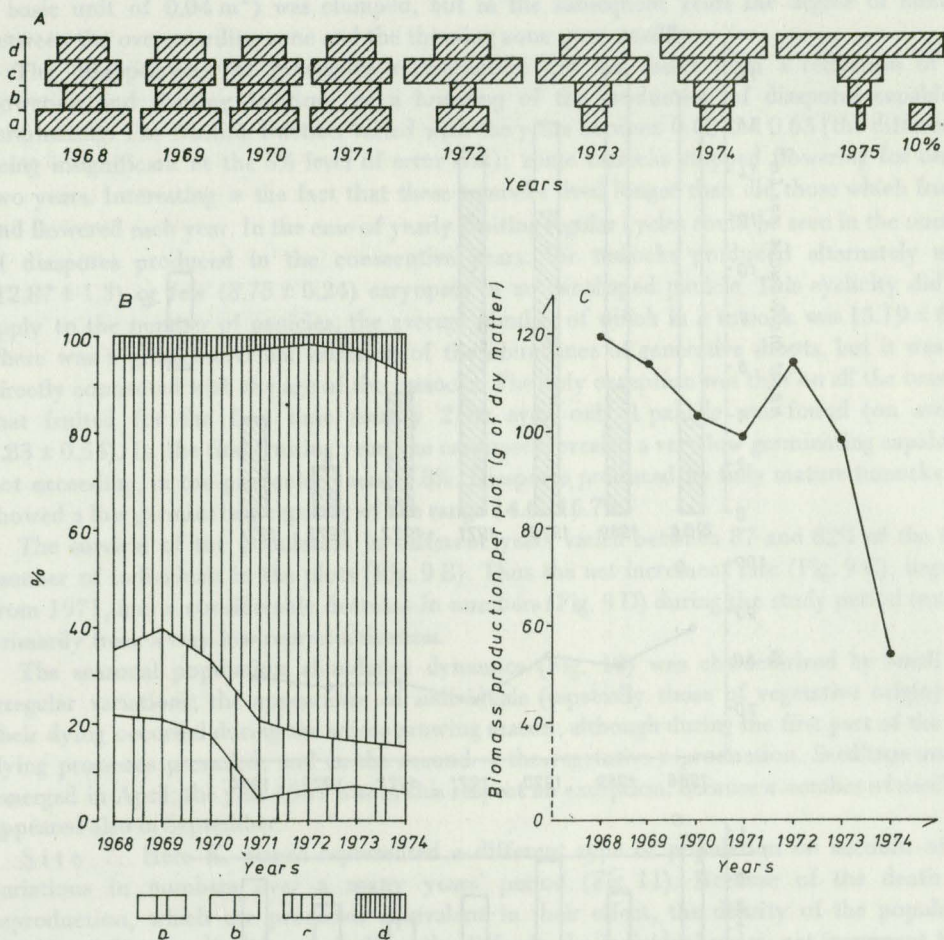


Fig. 8. Age spectrum of population (A), contribution of different age individuals to the production of biomass (B), and biomass production (C) of *Koeleria glauca* population on site 6
 Age groups of individuals: a – this year's, emerged from seeds and vegetatively, b – juvenile, c – mature, d – senile

The switching over of the *K. glauca* population from simultaneous generative and vegetative reproduction (during the first four study years) to exclusively vegetative reproduction (in the remaining study years) proceeded gradually, and was preceded by both a decrease in the number of seedlings (Fig. 9 A) and a decrease in their survival rate from year to year; in 1971, all seedlings died after 1–2 months. As a result of the high mortality of the seedlings (on an average 96.5% yearly), the life span of an average individual derived from seed was only 0.94 of a year (11 months and 7 days), while that of the individuals derived from vegetative reproduction – on an average 10.2 ± 3.6 years. In the last group the individual periods constituted the following percentage of the total length of the life cycle: pre-reproductive period – 28.1, reproductive maturity period – 49.0, post-reproductive period – 22.9.

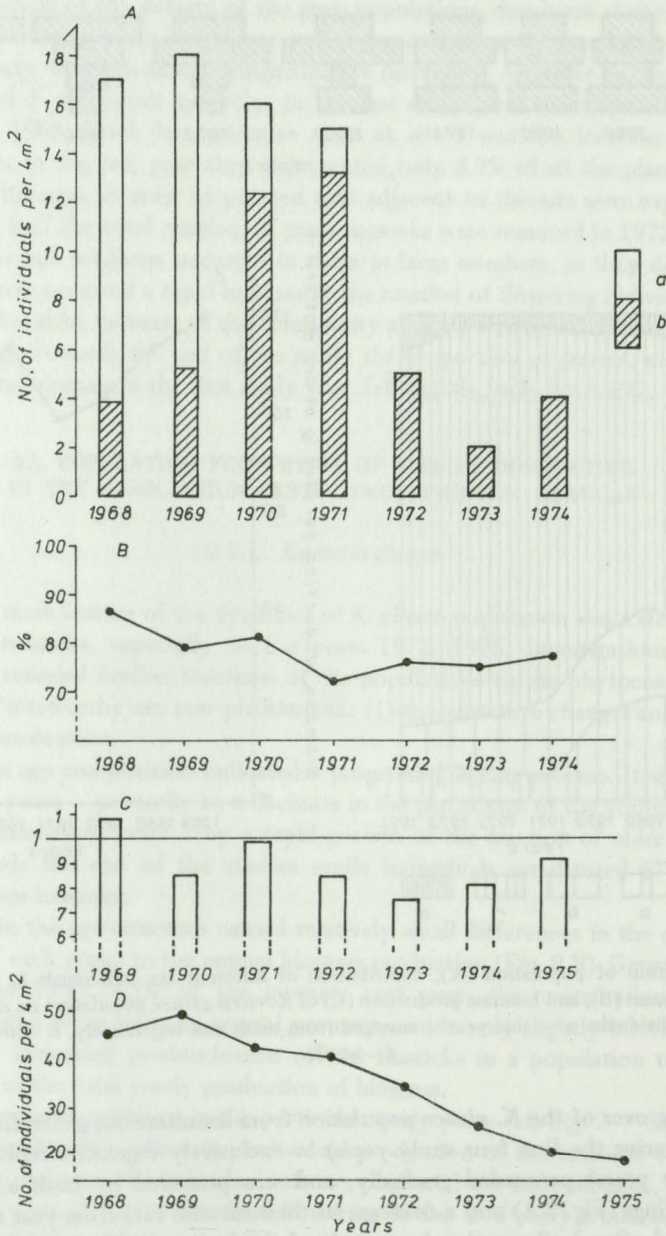


Fig. 9. Indices of population abundance dynamics of *Koeleria glauca* on site 6

A – reproductiveness, as expressed by the number of seedlings (a) and propagules (b) in a plot, B – survival, C – net increase (the ratio of population numbers in current year to population numbers in the fruiting period of the preceding year), D – population abundance during the fruiting period

Regardless of the method of reproduction, the type of spatial structure over the plots (with a basic unit of 0.04 m^2) was clumped, but in the subsequent years the degree of contrast between the overcrowding zone and the thinning zone grew steadily.

The disappearance of generative reproduction did not result from a reduction of the flowering and fruiting fraction, or a lowering of the production of diaspores capable of germinating. The fruiting fraction varied with the years between 0.42 and 0.65 (the differences being insignificant at the 5% level of error risk); some tussocks stopped flowering for one or two years. Interesting is the fact that these tussocks lived longer than did those which fruited and flowered each year. In the case of yearly fruiting regular cycles could be seen in the number of diaspores produced in the consecutive years: the tussocks produced alternately many (12.87 ± 1.3) or few (3.75 ± 0.24) caryopses in an ear-shaped panicle. This cyclicity did not apply to the number of panicles, the average number of which in a tussock was 15.19 ± 6.05 . There was a great individual variation of the abundance of generative shoots, but it was not directly connected with the age of the tussocks. The only exception was that on all the tussocks that fruited for the first time usually 2 or even only 1 panicle was found (on average 1.83 ± 0.54). In the first fruiting year, the caryopses revealed a very low germinating capability, not exceeding, in the particular years, 1.8%. Diaspores produced by fully mature tussocks also showed a low germinating capacity of the range 14.6–16.7%.

The survival of the population in different years varied between 87 and 82% of the total number of individuals in the plots (Fig. 9 B). Thus the net increment rate (Fig. 9 C), negative from 1971, and a considerable decrease in numbers (Fig. 9 D) during the study period resulted primarily from a very low reproductiveness.

The seasonal population abundance dynamics (Fig. 10) was characterized by small and irregular variations; the appearance of individuals (especially those of vegetative origin) and their dying occurred during the whole growing season, although during the first part of the year dying processes prevailed, and in the second – the vegetative reproduction. Seedlings usually emerged in April; the year 1969 was in this respect an exception, because a number of seedlings appeared also in September.

Site 7. Here *K. glauca* represented a different type of population on account of the variations in numbers over a many years' period (Fig. 11). Because of the death and reproduction, which are processes equivalent in their effect, the density of the population ($54.37 \pm 1.91 \text{ per m}^2$) did not significantly differ in the individual years, net increment being always close to unity, though always negative.

The reproduction of the population, very low throughout the study period (5–7 new individuals a year per m^2), was accomplished only by vegetative reproduction; in the plots, the clumped spatial structure was even more strongly marked than at site 6. New tussocks appeared early in autumn, less often in May or June.

Among the few individuals that died each year old tussocks predominated (61.2%). In four plots (16 m^2) a total of 13 this year's tussocks died during the eight study years, 6 in the second or third year of life, and 30 senile tussocks. Thus the number of individuals was not reduced by even one mature tussock: flowering and fruiting.

Apart from the maintaining of a stable level of numbers, the stabilized state of the *K. glauca* population on site 7 was further indicated by the following features, insignificantly varying statistically: (1) the flowering fraction ($51.37 \pm 4.27\%$), (2) diaspore production ($1313.6 \pm 11.26 \text{ per } 4 \text{ m}^2$), and (3) biomass production ($109.75 \pm 4.7 \text{ g dry weight per plot}$).

Most variable in the particular years was the age composition of the population (Fig. 11 A). None of the age groups showed permanent tendencies to increase or decrease its proportion in the total number of individuals, or biomass production (Fig. 11 B).

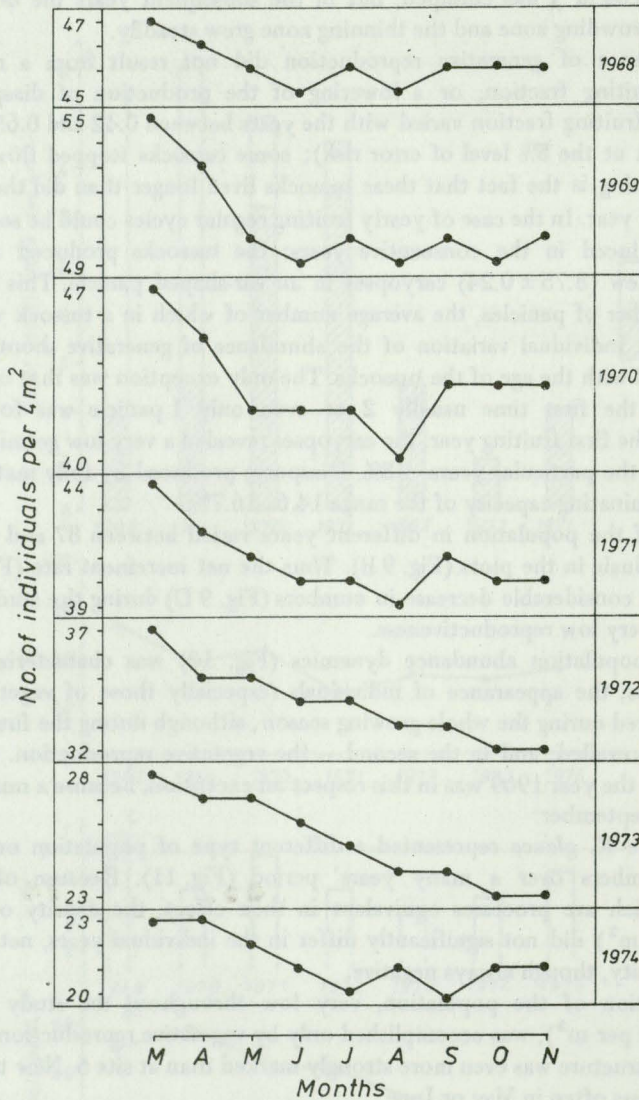


Fig. 10. Seasonal abundance dynamics of *Koeleria glauca* population on site 6

Comparing with the population 6 the complete life cycle of an average individual was somewhat longer (10.43 ± 3.7 years), but longer was only the pre-reproductive period (about a year), whereas the remaining life periods were proportionately shorter (Fig. 11 C).

An approximate estimation of the mortality of *K. glauca* individuals, depending on their age, was made in the following way: (1) In the first study year 100 individuals were selected for further study at site 7. These were individuals which had appeared in 1968 only as a result of

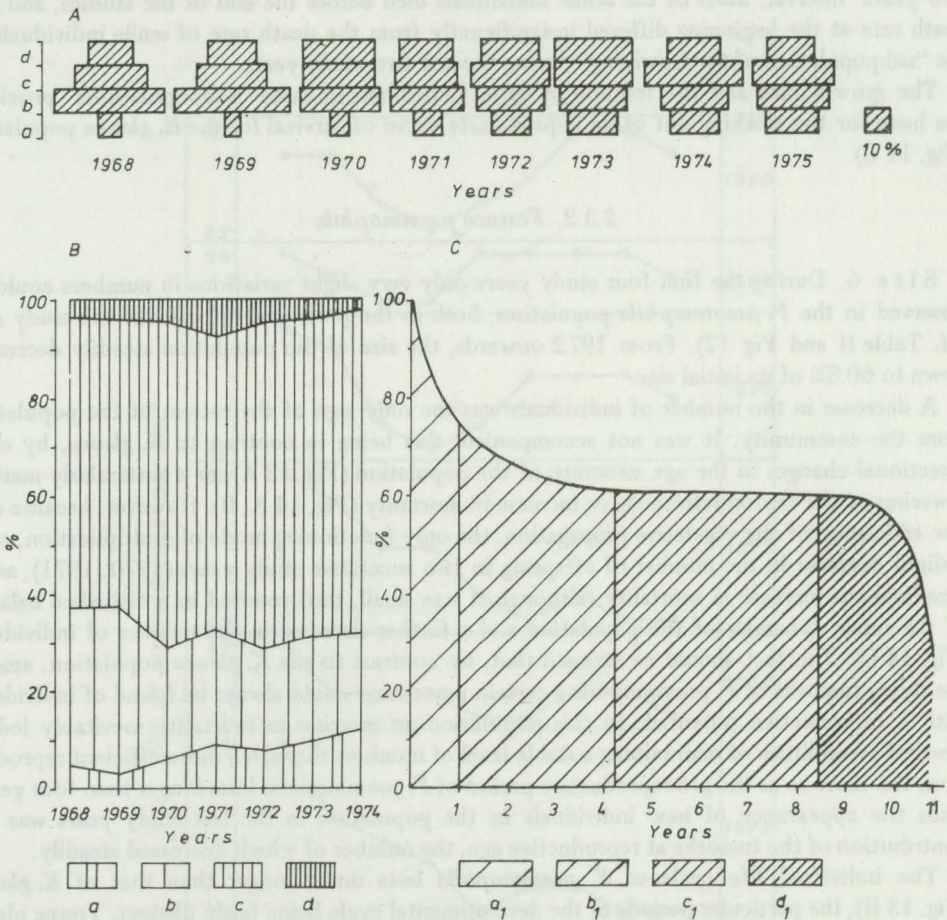


Fig. 11. Age spectrum of population (A), contribution of different age individuals to biomass production (B), and an approximate survival curve (C) for *Koeleria glauca* population on site 7. Age groups of individuals (a–d) as in Figure 8. Periods of life history: a_1 – period of fixing of young tussocks, b_1 – juvenile, c_1 – of generative maturity, d_1 – senile

vegetative propagation. For this group the “subpopulation of the young” – the dying fraction and the individual growth rate were determined during the successive seven growing seasons; the average age of attaining reproductive maturity was 4.2 years. (2) In the following year, 1969, another group of 100 was selected which included individuals that produced generative shoots for the first time. On the basis of this group (the “subpopulation of the flowering”) the average age of attaining the senile phase (8.4 years), the fraction of the survival of reproductively mature individuals and the fraction of the survival of individuals in an early senile stage were determined. (3) Also in 1969, the last group of 100 was selected consisting of individuals which were not flowering any more and showed clear signs of ageing; all the tussocks flowered and fruited a year earlier. Over ten tussocks were excluded from the estimation of the death rate for

this group, because they were found to have produced new generative shoots after a year's or two years' interval. Most of the senile individuals died before the end of the studies, and the death rate at the beginning differed insignificantly from the death rate of senile individuals of the "subpopulation of the flowering" during the last two study years.

The growth rate and the fraction of dying individuals in three "subpopulations" provided the basis for the working out of an approximate curve of survival for the *K. glauca* population (Fig. 11 C).

2.3.2. *Festuca psammophila*

Site 6. During the first four study years only very slight variations in numbers could be observed in the *F. psammophila* population, both in the plots and throughout the study area (cf. Table II and Fig 12). From 1972 onwards, the size of the population steadily decreased down to 60.8% of its initial size.

A decrease in the number of individuals was the only sign of the retreat of the population from the community. It was not accompanied, this being in contrast to *K. glauca*, by clear directional changes in the age structure of the population (Fig. 13 A), or a particularly marked lowering of the reproductiveness, or increase in mortality (Fig. 14 A, B). However, because of a low efficiency of the vegetative propagation, the only functioning mode of multiplication, even a slight decrease in the number of offspring in two successive study years (1970, 1971), and a simultaneous increase in mortality (although it was small, too) resulted in a disturbed balance of the inner dynamics of the population and a further decrease in the number of individuals (Fig. 14 C). The fact should be stressed that, by contrast to the *K. glauca* population, among the dying tussocks of *F. psammophila* a certain percentage could always be found of individuals with a reproductive potential; in this population an increase in mortality inevitably led to lowered possibilities of maintaining a stable level of numbers through a more efficient reproduction, the more so as the pre-reproductive period of *F. psammophila* lasts longer than four years. Thus the appearance of new individuals in the population in the last study years was the contribution of the tussocks at reproductive age, the number of which decreased steadily.

The individual life cycle of *F. psammophila* lasts much longer than that of *K. glauca* (Fig. 13 B), the particular periods of the developmental cycle being fairly distinct. Young plants retain the appearance of seedlings for more than two years. In the next two years they grew intensively forming distinct tussocks, each with a small number of panicles (2.38 ± 0.32) in whose spikelets only sporadically were caryopses produced. It is only in the fifth year of its life that *F. psammophila* attains the capability of maximum production of biomass, maturity for vegetative propagation, and full generative maturity. Mature tussocks produce a large, but very variable from year to year, number of panicles (on the average 13.8 ± 4.7), always with only a few caryopses (8.19 ± 1.7) in an average panicle. Peculiar to the senile age is a rapid decrease in both the total biomass production and the number of generative shoots; senile individuals do not propagate vegetatively either. Mortality risk is a permanent feature of a *F. psammophila* population, independent of the age of the individuals and their developmental stage; the survival curve, worked out in a way similar to that used for *K. glauca*, shows a gentle sloping corresponding to the whole life of the initial population (Fig. 13 B).

The production of biomass was lower than that of *K. glauca*: an average individual of *F. psammophila* produced about 0.81 g dry weight less than did an average tussock of *K. glauca*. A considerable decrease in the total production of biomass in the *F. psammophila* population, noticeable — by contrast to numbers — as early as the second study year

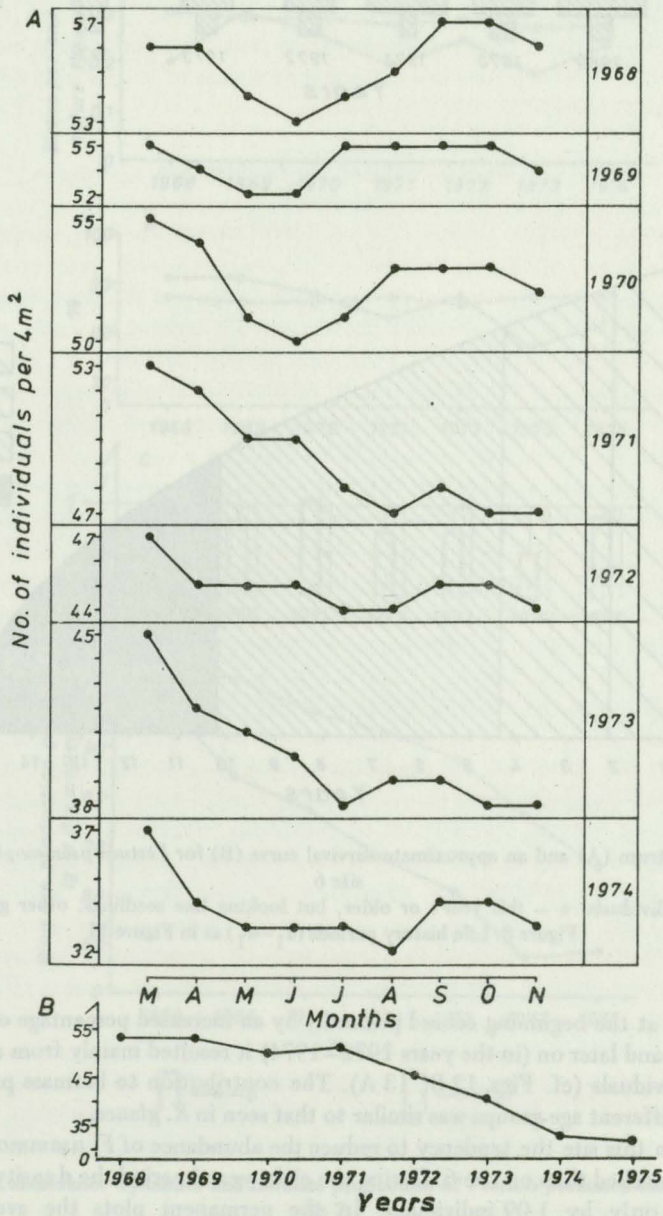


Fig. 12. Seasonal (A) and many years' (B) dynamics of *Festuca psammophila* population on site 6

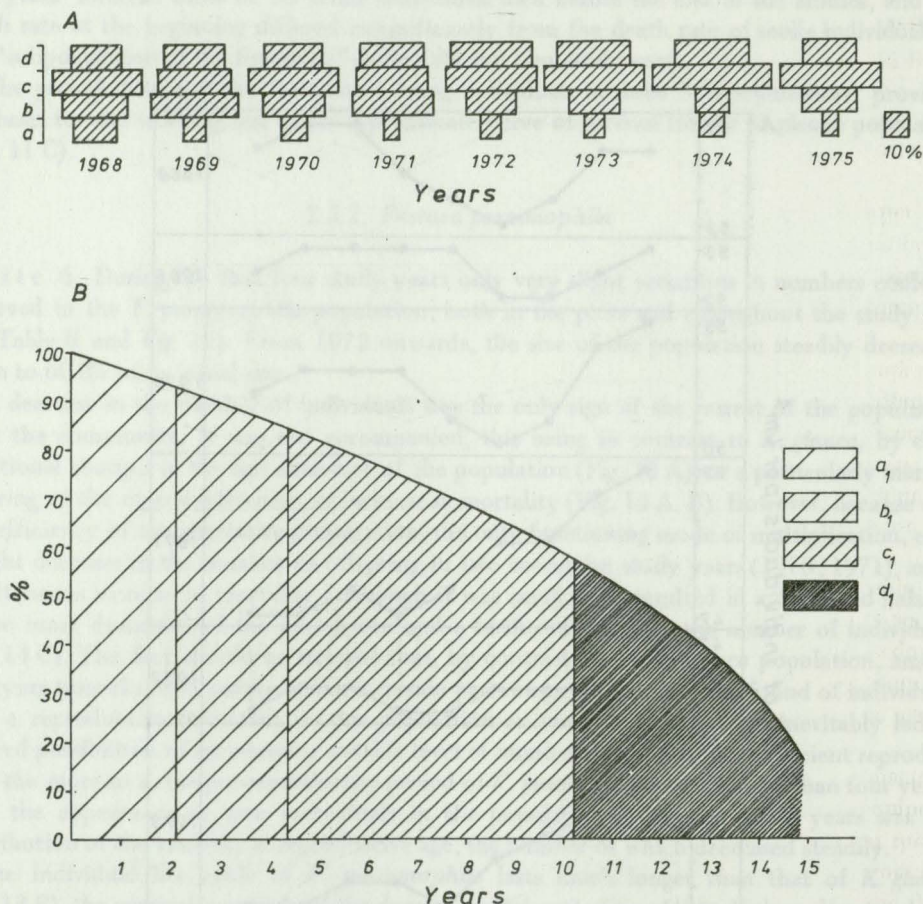


Fig. 13. Age spectrum (A) and an approximate survival curve (B) for *Festuca psammophila* population on site 6

Age groups of individuals: a — this year's or older, but looking like seedlings; other groups (b–d) as in Figure 8. Life history periods (a_1 – d_1) as in Figure 11

(Fig. 14 D) was at the beginning caused primarily by an increased percentage of old tussocks in the population, and later on (in the years 1972–1974) it resulted mainly from a lowering of the number of individuals (cf. Figs. 12 B, 13 A). The contribution to biomass production of the individuals of different age-groups was similar to that seen in *K. glauca*.

Site 7. On this site the tendency to reduce the abundance of *F. psammophila* population was much less marked than on site 6. During the eight years' period the density per 1 m^2 was at site 7 reduced only by 1.09 individuals. In the permanent plots the average number of individuals during the flowering period amounted to 52.37 ± 1.5 , and did not differ significantly between the individual years. No variation could be seen in the frequency of the tussocks either, neither at the site as a whole, nor in the study plots. The reproductiveness,

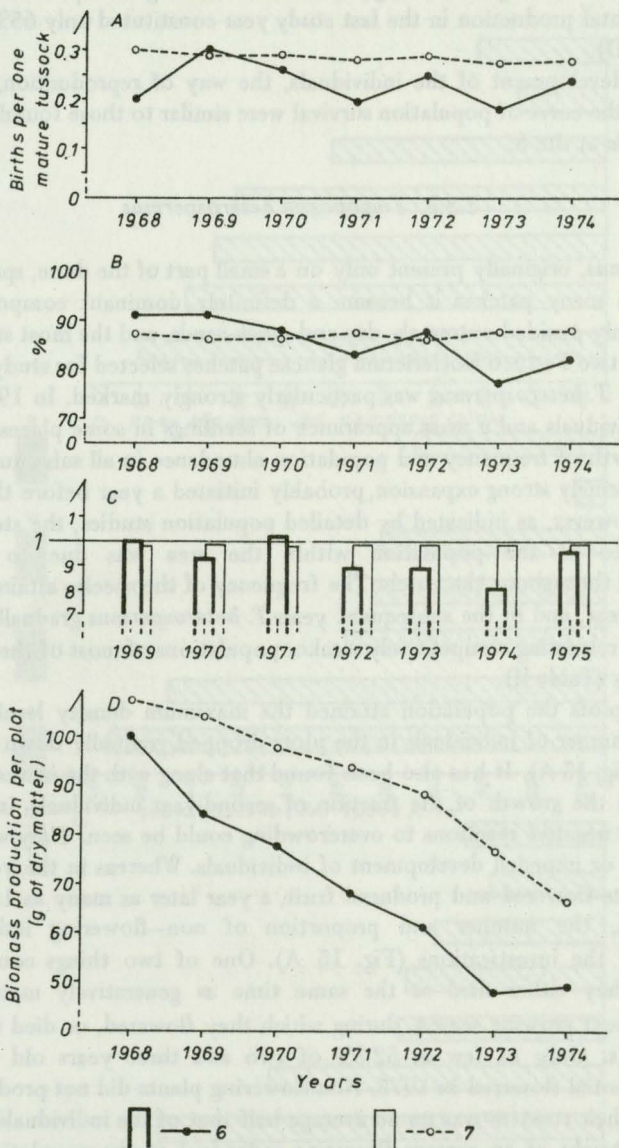


Fig. 14. Indices of abundance dynamics and biomass production of *Festuca psammophila* on site 6 and on site 7

A — reproductiveness, B — survival, C — net increase (cf. Fig. 9), D — biomass production

mortality and net increment of the population varied very slightly from year to year (Fig. 14 A, B, C).

More marked was the decrease in biomass production, especially in the groups of juvenile and old individuals. Although the changes in numbers and age composition of the population were small, the total production in the last study year constituted only 65% of the production of 1968 (Fig. 14 D).

The rate of development of the individuals, the way of reproduction, value of diaspore production, and the curve of population survival were similar to those found for the population of *F. psammophila* at site 6.

2.3.3. *Tragopogon heterospermus*

T. heterospermus, originally present only on a small part of the dune, spread almost all over the area, and in many patches it became a definitely dominant component of the plant community. It only avoided extremely dry and quick-sands, and the most strongly turfed sods.

On one of the two *Festuco-Koelerietum glaucae* patches selected for study, namely on site 6, the dynamism of *T. heterospermus* was particularly strongly marked. In 1968, a small number of flowering individuals and a mass appearance of seedlings in some places over the area, and then a rapid growth of frequency and population abundance in all subsequent years (Table II) indicated an extremely strong expansion, probably initiated a year before the beginning of the investigations. However, as indicated by detailed population studies, the steady increase in the overall abundance of the population within the area was due to the spreading of *T. heterospermus* throughout the patch. The frequency of the species attained 100% already in the third study year, and in the subsequent years *T. heterospermus* gradually colonized all free areas left by the retreating competitively weaker populations of most of the initial components of the community (Table II).

In individual plots the population attained the maximum density level within 4–5 years, whereafter the number of individuals in the plots dropped gradually down to about 82.4% of the peak level (Fig. 15 A). It has also been found that along with the increase in density and – above all – with the growth of the fraction of second-year individuals, in the population of *T. heterospermus* negative reactions to overcrowding could be seen. They were manifested by:

1. A retarded or impeded development of individuals. Whereas in the years 1969–1971 all second-year plants flowered and produced fruit, a year later as many as 15.2% of individuals remained barren, the number and proportion of non-flowering individuals increasing until the end of the investigations (Fig. 15 A). One of two things could happen to those individuals: they either died at the same time as generatively mature individuals, or survived till the next growing season, during which they flowered, or died in the third year as barren individuals. Only as few as 52.3% of two and three years old individuals with a reproductive potential flowered in 1975. Non-flowering plants did not produce stems, whereas the diameter of their rosettes was on an average half that of the individuals able to reproduce.
2. A smaller height of an average flowering individual of the population (Fig. 15 B), and smaller differences between the extreme heights of individuals in the population.
3. A decreased number of heads (Fig. 15 C).
4. A decreased number of diaspores in heads (Fig. 15 D).

The correlation coefficients for the number of flowering individuals in a plot, and for the height, the number of infructescences and of diaspores in one head of an average individual in the population in the years compared were: -0.96 , -0.89 and -0.81 , respectively; thus in all cases the effect of overcrowding appeared to be significant. The particularly low values, in 1974, of

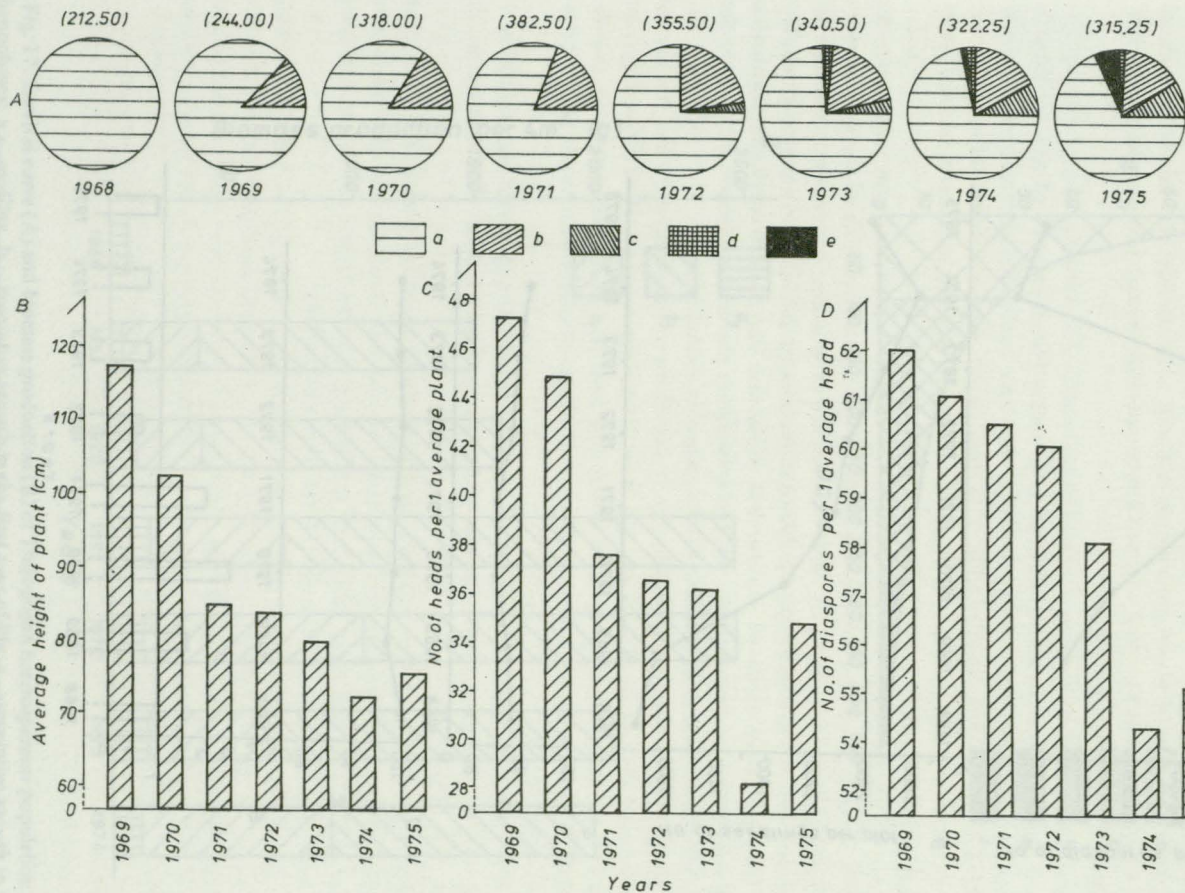


Fig. 15. Age spectrum (A) and some morphological features of an average flowering individual (B–D) of *Tragopogon heterospermus* population on site 6. Individuals: a – seedlings, b – second year's flowering, c – second year's non-flowering, d – three years old flowering, e – three years old non-flowering. Numbers in brackets denote average density in plots during the fruiting period

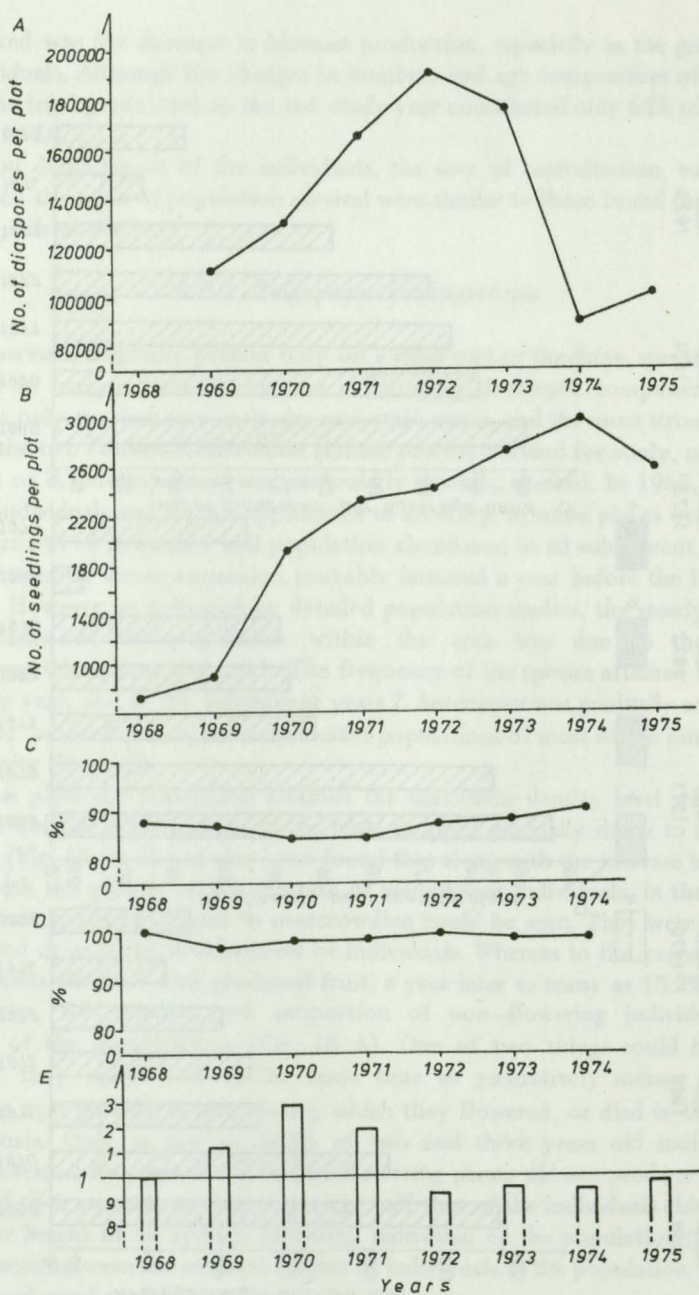


Fig. 16. Indices of population dynamics of *Tragopogon heterospermus* on site 6
 A - diaspore production, B - reproductiveness, C - mortality, D - percentage of seedlings in the total number of dead individuals, E - net increase

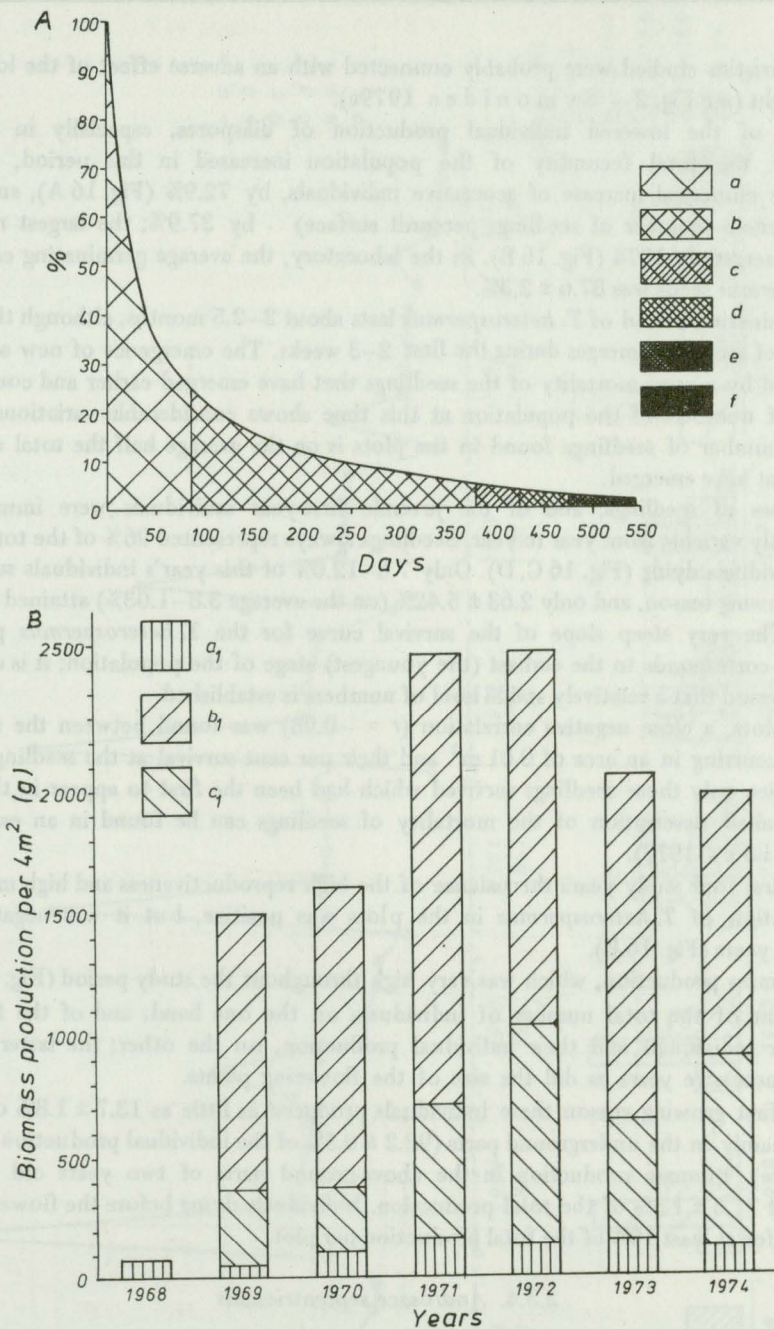


Fig. 17. Survival curve (A) and biomass production (B) of *Tragopogon heterospermus* population on site 6 Phenophases: a – seedling, b – vegetative growth in the first year of life, c – vegetative growth in the second year of life, d – budding, e – flowering, f – fruiting. 100% – average number of seedlings in an area of 4 m² in the years 1968–1974. The points on the curve – an average percentage of individuals dying in successive time intervals. In the working-out of the curve individuals which survived up to the third growing season were not taken into account. Proportions of the biomass: a₁ – biomass of first-year individuals, b₁ – biomass of above-ground parts of second-year individuals, c₁ – biomass of underground parts of second-year individuals

the characteristics studied were probably connected with an adverse effect of the long-lasting spring drought (see Fig. 2 — Symonides 1979a).

In spite of the lowered individual production of diaspores, especially in the years 1969–1972, the total fecundity of the population increased in this period, due to a considerable numerical increase of generative individuals, by 72.9% (Fig. 16 A), and the real reproductiveness (number of seedlings per unit surface) — by 37.9%; the largest number of seedlings emerged in 1974 (Fig. 16 B). In the laboratory, the average germinating capacity of *T. heterospermus* seeds was $87.6 \pm 2.3\%$.

The germinating period of *T. heterospermus* lasts about 2–2.5 months, although the highest percentage of seedlings emerges during the first 2–3 weeks. The emergence of new seedlings is accompanied by a mass mortality of the seedlings that have emerged earlier and consequently the level of numbers of the population at this time shows considerable variations, and the maximum number of seedlings found in the plots is on the average half the total number of seedlings that have emerged.

The losses of seedlings, and of the juvenile first-year individuals were immense, but insignificantly variable from year to year. Seedlings always represented 96% of the total number of the individuals dying (Fig. 16 C, D). Only 7.6–12.0% of this year's individuals survived till the next growing season, and only $2.63 \pm 5.42\%$ (on the average $3.8-1.03\%$) attained generative maturity. The very steep slope of the survival curve for the *T. heterospermus* population (Fig. 17 A) corresponds to the earliest (the youngest) stage of the population; it is only in the flowering period that a relatively stable level of numbers is established.

In the plots, a close negative correlation ($r = -0.98$) was found between the number of seedlings occurring in an area of 0.01 m^2 and their per cent survival at the seedling stage. At high densities only those seedlings survived which had been the first to appear in the population. A detailed description of the mortality of seedlings can be found in an earlier paper (Symonides 1977).

In the first four study years the balance of the high reproductiveness and high mortality of the population of *T. heterospermus* in the plots was positive, but it was negative in the subsequent years (Fig. 16 E).

The biomass production, which was very high throughout the study period (Fig. 17 B), was the resultant of the total number of individuals on the one hand, and of the fraction of second-year individuals and their individual production, on the other; the latter decreased with the successive years as did the size of the flowering plants.

In the first growing season these individuals produced as little as $13.7 \pm 1.8\%$ of the total biomass, mainly in the underground parts ($92.2 \pm 0.5\%$ of the individual production in the first year of life). Biomass production in the above-ground parts of two years old individuals represented $77.3 \pm 1.3\%$ of the total production. Individuals dying before the flowering period accounted for at least 10% of the total production per plot.

2.3.4. *Androsace septentrionalis*

A. septentrionalis was found only in several patches of Spergulo-Corynephorretum and Festuco-Koelerietum glaucae, most often in small numbers. Only on site 6 did it grow and flower in large numbers, giving a vernal aspect to the community, "old" in this time of the year. Here *A. septentrionalis* belonged to the few species which persisted throughout the study period, although in the last two years they occurred in much reduced numbers of individuals

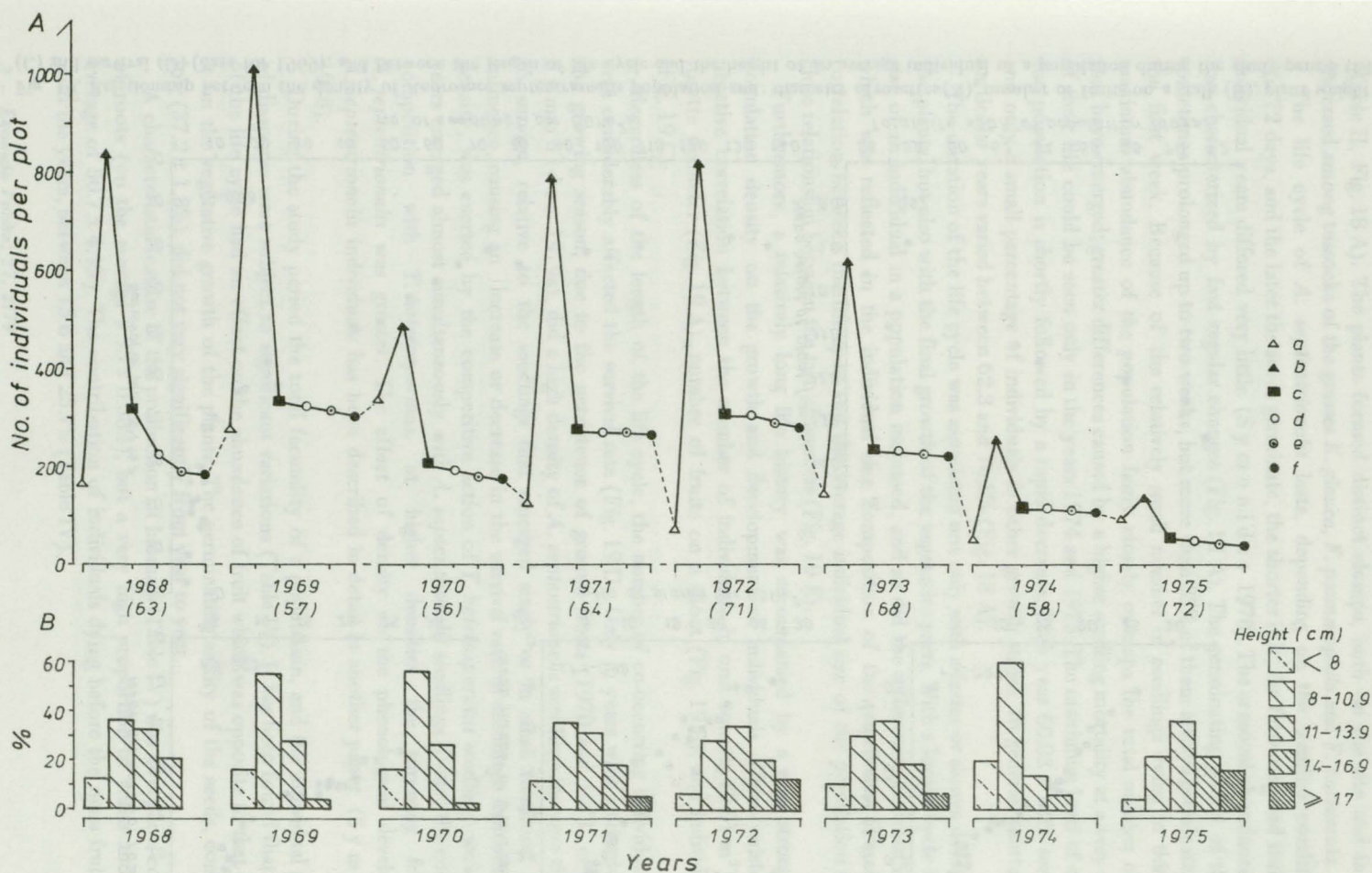


Fig. 18. Seasonal and many years' population dynamics (A) and the percentage of different size individuals in the population (B) of *Androsace septentrionalis* on site 6
Phenophases: a – beginning of germination, b – maximum germination, c – end of seedling phase, d – period of vegetative growth, e – flowering, f – fruiting. Numbers in brackets – total life span of the population in the particular year (in days)

(Table II, Fig. 18 A). The plants formed distinct clumps, both on the site and in the plots, dispersed among tussocks of the grasses *K. glauca*, *F. psammophila* and *F. duriuscula*.

The life cycle of *A. septentrionalis* lasts, depending on the weather conditions, only 56–72 days, and the later the seeds germinate, the shorter it is; the flowering and fruiting in the individual years differed very little (S y m o n i d e s 1978). The seasonal abundance dynamics was characterized by fast regular changes (Fig. 18 A). The germinating period of the seeds is sometimes prolonged up to two weeks, but more than 85% of them always germinate already in the first week. Because of the relatively small number of seedlings dying in this time, the maximum abundance of the population fairly closely overlaps the total number of seedlings that have emerged; greater differences caused by a higher seedling mortality at a very early stage of their life could be seen only in the years 1974 and 1975. The maximum level of numbers of the population is shortly followed by a rapid decrease. Each year $60.03 \pm 1.2\%$ seedlings die, and only a small percentage of individuals in other growth stages. In general, mortality in the particular years varied between 62.3 and 76.8% (Fig. 18 A).

The duration of the life cycle was associated not only with a faster or slower development of the plants, but also with the final growth of the vegetative parts. With a longer cycle the average size of an individual in a population increased, and so did the differences between individuals, which was reflected in the individual size composition of the population (Fig. 18 B). The correlation between the life span and the average individual size of the population indicated a close relationship between the two characters (Fig. 19 E).

Furthermore, a relatively long life history was accompanied by a very strong effect of population density on the growth and development of individuals. There existed a close negative correlation between the number of individuals in unit squares (0.01 m^2) and: leaf rosette diameter (Fig. 19 A), number of fruits on a shoot (Fig. 19 B), and individual weight (Fig. 19 C).

Regardless of the length of the life cycle, the number of co-occurring individuals per unit area considerably affected the survival rate (Fig. 19 D). Only in years with a retarded onset of the growing season, due to the persistence of ground frosts (1970 and 1971, cf. Fig. 2 — S y m o n i d e s 1979a), did a high density of *A. septentrionalis* seedlings increase their chance to survive, relative to the seedlings that emerged singly or in small densities. Additional influence, causing an increase or decrease in the survival rate of seedlings, depending on their density, was exerted by the competitive action of *T. heterospermus* seedlings which in those years emerged almost simultaneously with *A. septentrionalis* seedlings. Under the conditions of competition with *T. heterospermus*, at higher densities the surviving fraction of *A. septentrionalis* was greater. The effect of density on the phenological development of *A. septentrionalis* individuals has been described in detail in another paper (S y m o n i d e s 1978).

During the study period the total fecundity of a population, and the individual production of diaspores were subject to significant variations (Table IV). It has been found that the length of the life cycle had an effect on the abundance of fruit which was opposite to that exerted by it on the vegetative growth of the plants. The germinating ability of the seeds, comparatively low ($37.2 \pm 1.8\%$), did not vary significantly from year to year.

A characteristic feature of the production of biomass (Table IV) was a very low contribution of roots (on the average $9.93 \pm 0.58\%$), but a very high proportion of fruits and seeds (an average of $50.7 \pm 4.4\%$). The contribution of individuals dying before the mass fruiting varied with the years, between 15.6 and 25.7% (Table IV).

Table IV. Production of diaspores and of biomass by a population of *Androsace septentrionalis* (site 6)

Year	Number of diaspores		Biomass production (g d. wt)			
	per an individual	per 1 m ² area (in thous.)	per 1 m ²	contribution of roots (%)	contribution of diaspores to production by fruiting individuals (%)	contribution of individuals which died before fruiting (%)
1968	1067.3	205.5	146.9	9.65	51.2	19.2
1969	1118.9	338.5	246.8	10.81	55.7	25.7
1970	1301.0	195.8	124.4	10.31	56.4	15.6
1971	962.4	285.8	202.2	9.41	46.6	21.1
1972	971.3	299.2	228.1	9.69	47.3	20.1
1973	956.5	217.6	184.3	9.04	47.7	18.2
1974	1068.7	120.2	72.4	10.13	54.8	21.6
1975	952.4	34.3	36.7	10.4	45.6	16.7

2.4. THE DYNAMICS OF SEMISYNANTHROPIC DUNE COMMUNITIES AS EXEMPLIFIED BY CORISPERMO-PLANTAGINETUM INDICAE

The site (8) to be used for investigations into the ecology of the association Corispermo-Plantaginetum indicae was located within a fairly large and floristically rich patch, in the north-eastern portion of the dune near a site where a poultry farm was being built. Outside this patch, the association was represented only by communities, poor in species, on small areas usually near buildings, roads, and railways.

In respect of both the specific composition and dynamics the association Corispermo-Plantaginetum indicae differed considerably from all the other psammophyte communities taken into account in the present research. The number of species and the floristic composition (Table V), as well as the abundance of their populations varied noticeably from year to year, all the changes being of the nature of irregular fluctuations. Out of the 25 species, recorded from an area of 100 m², only 5 species occurred throughout the study period.

The most important structure features of the community are as follows: (1) a large percentage of annuals and biennials the total number of which represented each year 40.0–55.0% of the total numbers of the particular species; (2) a low frequency of species within an area; except for *P. indica*, whose population attained, at least in some years, over 40% frequency (Fig. 20 A), all the species formed only a few, as a rule unispecific, clumps clearly separated from one another with bare sand; (3) a low and varying, from year to year, coverage of the surface amounting from 40 up to 45%, and (4) a complete lack of the layer of mosses and lichens.

Although the qualitative and quantitative composition of the community changed from year to year, the total biomass of the vegetation in the study years compared differed insignificantly. In the period of fruiting of most of the plants in the area it varied between 4.62 and 5.76 kg. Over 70% of the biomass was contributed by the grasses: *Corynephorus canescens* and *Festuca psammophila*.

Table V. Specific composition and population numbers in a patch of *Corispermum-Plantaginum indicae**

Species	1968	1969	1970	1971	1972	1973	1974	1975
<i>Plantago indica</i>	774	56	418	270	209	1021	136	526
<i>Corispermum hyssopifolium</i> L.	27	317	185	0	0	76	212	21
<i>Corynephorus canescens</i>	212	278	246	217	185	167	142	141
<i>Artemisia campestris</i>	40	40	40	43	43	40	48	48
<i>Potentilla argentea</i> L.	15	15	17	21	21	21	18	14
<i>Festuca psammophila</i>	512	540	515	496	474	460	447	438
<i>Bromus tectorum</i> L.	75	415	760	211	55	0	111	315
<i>Carex caryophylla</i> Latourette	11	12	13	9	8	5	4	0
<i>Rumex acetosella</i>	36	27	20	11	0	0	7	17
<i>Trifolium arvense</i>	29	148	266	111	0	0	78	56
<i>Carex hirta</i>	6	6	5	4	0	0	0	0
<i>Oenothera biennis</i> L.	5	17	0	0	0	13	8	6
<i>Spergula vernalis</i>	1511	278	0	0	0	0	0	0
<i>Jasione montana</i>	15	9	0	0	0	0	0	0
<i>Sedum acre</i> L.	19	14	0	0	0	0	0	0
<i>Senecio vernalis</i> W. K.	0	45	0	0	27	0	78	11
<i>Arabis arenosa</i> (L.) Scop.	0	34	0	0	21	0	36	0
<i>Erigeron canadensis</i> L.	0	36	125	0	456	36	75	128
<i>Salsola kali</i> L.	0	0	215	540	185	0	21	0
<i>Capsella bursa-pastoris</i> (L.) Med.	0	0	11	25	0	78	165	94
<i>Anchusa officinalis</i> L.	0	0	0	36	47	0	0	0
<i>Erodium cicutarium</i> (L.) L'Herit	0	0	0	0	7	0	21	14
<i>Linaria vulgaris</i> (L.) Mill.	0	0	0	0	7	9	13	15
<i>Taraxacum officinale</i> Web.	0	0	0	0	8	11	46	54
<i>Poa annua</i> L.	0	0	0	0	0	0	7	9
Total number of species	15	18	14	13	15	13	20	17
Total number of individuals	3287	2287	2836	1994	1733	1937	1673	1907
Proportions of annuals and biennials (%)	40.0	50.0	50.0	46.1	53.3	41.7	55.0	52.9

*Seedlings have not been taken into account.

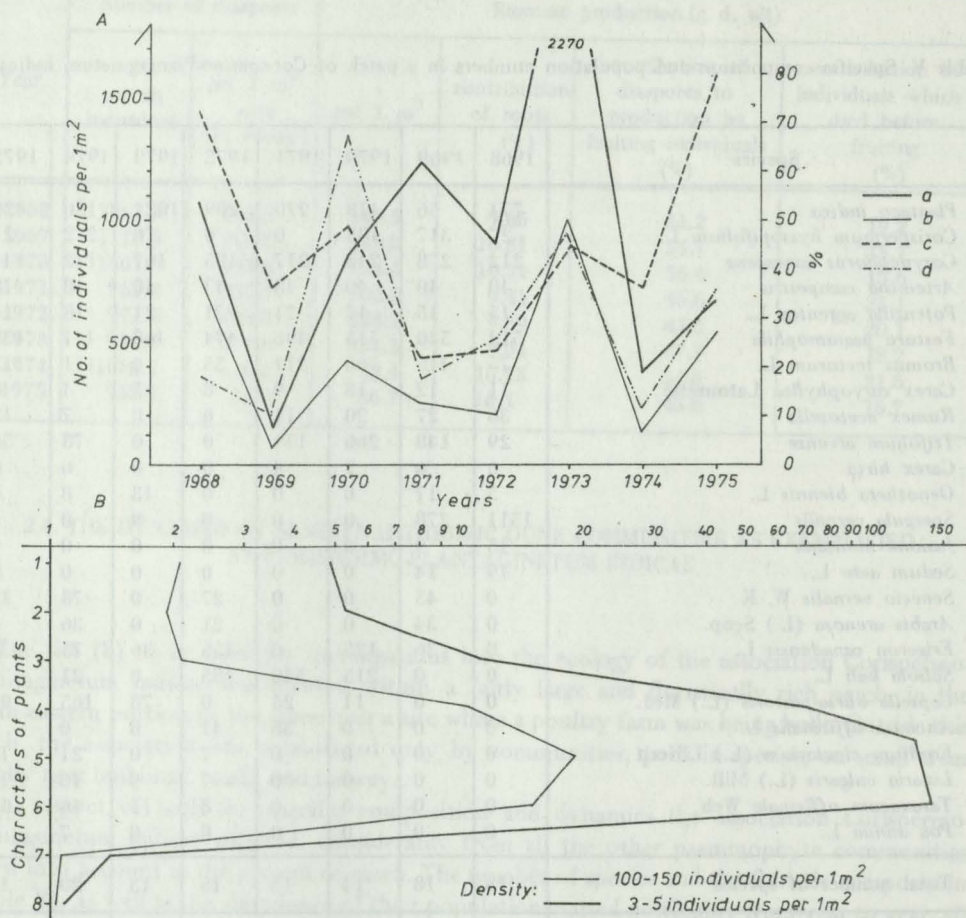


Fig. 20. Number of seedlings (a), and of flowering individuals (b), population survival (c) and frequency (d) of *Plantago indica* in a patch of *Corispermum-Plantaginietum indicae* (A), and the effect of population density on morphological characteristics of an average individual (B)

Unit of comparison – characters of an average individual at a density equal to, or greater than 300 individuals per 1 m². Characters: 1 – stem length, 2 – root length, 3 – breadth of plant, 4 – number of lateral ramifications, 5 – number of infructescences, 6 – weight of plant, 7 – number of seeds in one infructescence, 8 – seed weight. Comparison of morphological characters of the individuals of a population was made by the method of Jentys-Szaferowa (1959)

2.5. POPULATIONAL AND INDIVIDUAL VARIATION OF *PLANTAGO INDICA*

P. indica occurred in small numbers nearly in all the area of the dune, most often as an accompanying species in patches of the associations *Spergulo-Corynephorretum* and *Festuco-Koelerietum glaucae*. However, it finds its ecological optimum conditions in loose,

semisynanthropic communities, typologically similar to *Corispermo-Plantaginetum indicae*, or *Bromo-Corispermetum Siss et Westh.* 1946, in which it sometimes occurs in large numbers, the individual plants being of particularly good shape.

In *Corispermo-Plantaginetum indicae* community on site 8 the *P. indica* population showed a considerable variation with time and space, in respect of both the frequency and numbers (Fig. 20 A), and the habitus and size of the individuals, and even the survival, rate of phenological development, and many other morphological or biological properties.

The number of seedlings in different plots ranged from over 700 to only a few. Noticeably variable was also the average density of seedlings in the particular years: from 69.4 in 1975 to 12.7 in 1970 per 1 m² surface area. The larger or smaller number of seedlings was not directly related to an abundance of fruits in the population in the preceding year, or to the type of weather conditions in given year. As can be seen also from Figure 20 A, the surviving fraction differed very considerably independently of the population density and the type of weather, different in each year. The correlation coefficient for the total number of seedlings and for the survival in the particular year (from $r = -0.016$ to $r = 0.031$) showed that there was no relationship whatsoever between these two characters. Furthermore, in the same year a different percentage of them died in each of the different plots, independently of the density. It suffices to point that in one of two plots with the same number of seedlings in 1968 as much as 99% died, and only 3.5% in the other. However, each year and in each plot dead seedlings constituted over 90% of the total number of dead individuals.

The density of the individuals that survived the seedling stage had a very significant effect on their final size, number of ramifications, weight and number of infructescences (Fig. 20 B). All these characteristics formed in a close, negative ($r =$ from -0.95 to $r = -0.98$) correlation with the number of individuals co-occurring in the same unit area. Worth mentioning, as a curiosity, is the fact that two very sizeable plants which emerged in 1974, at a density of 1 individual per 1 m² area, attained a height of 67.1 and 72.5 cm, a diameter of 63 and 74 cm, respectively, each of them produced 2.5 thousand infructescences, their joint weight being equal to that of the remaining 524 individuals on the site, which together had at their disposal only three times as large an area; in that year an average individual of the population, except the two "giants", attained a height of 12.3 ± 1.01 cm, a diameter of 5.2 ± 0.4 cm, and 13.3 ± 1.8 infructescences. The limiting effect of density on the height and weight of the individuals of *P. indica* was also seen when a dense clump of plants included also individuals of *Salsola kali*, in addition to *P. indica* (in 1970 and 1971).

Density was found to have a weaker and less univocal effect on the phenological development of *P. indica* individuals: up to a certain level of density there occurs an acceleration of the early phenological phases, whereas under the conditions of an extreme overcrowding (above 200 individuals per 0.01 m²) the plants did not attain the flowering phase, but they survived, as dwarfish plants till the period of mass dying of the remaining individuals of the population. Problems related to the course of the phenological development of *P. indica* individuals, depending on their density, have been discussed in detail in the paper by Symonides (1978).

The total diaspore production varied very clearly with the years; the plants produced the largest numbers of diaspores when the population consisted of a small number of individuals occupying a fairly large area. In 1969, in spite of the small numbers of individuals present, the total number of seeds was 1.7 times as large as in 1974 when the level of numbers (and density) in the population was almost ten times as high. *P. indica* seeds are characterized by a poor germinating capacity, not exceeding 15% under laboratory conditions. Thus the real repro-

ductiveness of a population represents one tenth per cent of the total, very high, fecundity, even after applying the correction of the germinating capacity.

Fruits with seeds account for as much as 37.5–40.9% of the biomass of *P. indica* plants, this being similar to the proportions in other annual species; the roots account for as little as 18% of the total biomass.

3. DISCUSSION

Loose psammophyte sods showed during the study period a considerable dynamics and a large variety of changes. An extreme effect of these changes was a complete reconstruction of the specific composition and significant changes in the quantitative relations between the populations of the species making up a community. In other patches directional changes were manifested only by a considerable decrease or increase in numbers of the individual species, with no basic changes in the composition of the community. Finally, both the qualitative and quantitative structure of the community were subject to considerable, irregular and non-directional variations from year to year; R a b o t n o v (1965) and V a s i l e v i č (1970) have suggested for changes of this type the names: "irregular oscillations" or "irregular fluctuations".

Directional changes in the composition and numbers of species occurred on sites 4 and 5, as a result of the encroachment and retreat, respectively, of *C. arenaria* from the sod. Assuming that the phenomena observed on site 5 after several years will have a similar course also on site 4, all the changes in both these areas jointly can be considered as the initial stage of succession of the association of *Spergulo-Corynephorum*. From the rate of "travelling" of a sedge sod, defining the rate of changes in the vegetation of the patch, it can also be concluded that a complete exchange of the specific composition over a surface area of 100 m² is realized during a period of over twenty years.

On the species making up the association *Spergulo-Corynephorum* only *F. duriuscula* builds also the framework of the new community. A small number of only young tussocks of *K. glauca* and *F. psammophila* at site 5 indicates that these two species had retreated as a result of the pressure of the sedge sod, and they colonized the sands again after the sedge had withdrawn. The remainder of the plants following the encroaching *C. arenaria* usually become component elements of a typical combination of species in the association *Diantho-Armerietum* or *Festuco-Koelerietum glaucae* (K r a u s c h 1968). It appears, therefore, that although it is only a transitional dominant species in loose psammophyte sods, *C. arenaria* is a permanent edifier causing significant changes in the biotope.

However, changes in the patch of *Festuco-Koelerietum glaucae* on site 6 cannot be considered in succession categories, although in their course a clear trend could be seen in the increase in numbers in the *T. heterospermus* and *F. duriuscula* populations, and the decrease of the species diversity of the community. In the patch there occurred an almost four-fold decrease in the number of species within as short a period as four years! However, characteristic species of the association persisted until the end of the studies (and in fairly large numbers), whereas no new elements, characteristic of other syntaxonomic units appeared there.

Unfavourable changes in the population of *T. heterospermus*, progressing with the growth of overcrowding (a retarded development of individuals, a lowered diaspore production, a weaker vegetative growth of vegetation) permit the conclusion that *T. heterospermus* is, like *C. arenaria*, only a transient dominant in loose sods, whereas, by contrast to *C. arenaria*, it does

not cause stable changes in the biotope. Following the removal of all individuals of *T. heterospermus* and yearly removal of seedlings, in the experimental plots a fast return was observed of most of the species which "lost" the competition with *T. heterospermus* during its dominance, and a fast increase in numbers in the populations of species which withstand the "invasion" of *T. heterospermus*. In the latter group a particularly intensive reproduction has been found for the grasses: *F. psammophila* and *F. duriuscula*. It should be noted that with a growing sodding, *Tragopogon* seedlings emerged less abundantly from year to year.

Changes observed in the second patch of *Festuco-Koelerietum glaucae* (on site 7) were primarily quantitative changes and changes associated with the inner dynamics of communities. During the period of several years no significant transformations in the specific composition, or the composition and structure of dominants took place. The total number of plants at the site varied insignificantly from year to year. However, a more exact analysis of the population dynamics of individual species revealed regular, though slow, changes in the community, which may be regarded to be symptoms of succession transformations. They concerned a gradual increase in numbers of the species making up primarily the very dense psammophyte communities (*Festuca duriuscula*, *Armeria elongata*, *Veronica spicata*, *Centaurea rhenana*), and at the same time indicated a slow decline of the populations of plants characteristic of loose, poorly overgrown sands (*Corynephorus canescens*, *Helichrysum arenarium*, *Hieracium pilosella*, *Sedum reflexum* and others). In the latter plant group, already from the middle of the study period no reproductive processes could be seen; only ageing individuals survived. Thus it may be concluded with a great caution that the succession of the community tends towards *Diantho-Armerietum*.

Significant, but difficult to interpret univocally, changes in the qualitative and quantitative structure of the community could be observed in the *Corispermo-Plantagnetum indicae* patch. Different each year was not only the set of species, but also the abundance of their populations, and, what is more, each year a different species attained numerical predominance over the remainder of species. Differences in the structure of the community, very distinct each year, resulted mainly from a high percentage of annual and biennial species, the numbers of which usually vary considerably with time (Salisbury 1942, 1952, Wilkoń-Michałska 1976, Falińska 1977). Non-directional and irregular, and at the same time clear changes in the specific composition and numbers of the particular species indicate weak phytocenotic relations between the components of the community, or a specific dynamics of the communities with a high percentage of short-living plants in which regularities of changes can only be demonstrated over a long period.

The populations of the species selected for the detailed studies also represented a variable dynamics. The populations of *T. heterospermus*, especially on site 6, and of *C. arenaria* on site 4 were characterized by an expansive growth lasting several years. In either case the efficiency of the spreading of the population was due, among other things, to a relatively low density of the vegetation in the "occupied" patches, and thereby -- to the wide area being available to the spreading populations. According to Gadgill (1971), this is the basic condition making possible not only the settling of a population in a new terrain, but also its growth in numbers. The important element on which the success of expansion depends is a fast rate of development and a high competitive power of the species (Harper 1977). At least several of the biological properties of *T. heterospermus* make it possible for the species to easily invade and colonize new territories: (1) a short development cycle of the plant, (2) a high rate production of diaspores with a high percent of germinating capacity, (3) anemochory, (4) diaspore structure: an elongate shape and presence of a pappus, (5) a large size of the

fruiting individuals. According to Harper (1977) and the authors quoted by him: Ridley (1930) and Van der Pijl (1969), characteristics (2) to (5) are most important for the dispersal of seeds, and they make it possible for the expansive species to colonize very distant areas.

T. heterospermus acts on other plants in the community through both a mechanical destruction and pressing down of smaller plants, and — above all — changes in the physical conditions of their growth. The latter effect is due to the considerable overdrying of the surface soil layers, this being the direct result of the sinking of rainfall water down the long taproots of *T. heterospermus* (Wilkoń-Michalska and Symonides 1974). The psammophytes, which usually are shallow-rooted (ombrophilic water balance), clearly suffered from shortage of water — as also from undernourishment — and they died rapidly. A joint action of drought and food stress causes particularly unfavourable changes in the plants, especially during their intensive growth (Grime and Curtis 1976), and, as a consequence, it was the young plants that died, being followed also by the older ones. Owing to their specific ability to retain water in the rhizosphere, *F. psammophila*, *F. duriuscula* and *K. glauca* were the only species that were able to survive; the “power” of *A. septentrionalis* probably lay in its short life cycle, completed entirely in the early spring period, when the soils are relatively well supplied with water; towards the end of the study the remaining species — *Artemisia campestris* and juvenile individuals of *Pinus sylvestris* — in spite of their strongly developed root systems, showed signs of dying.

In *C. arenaria* the course of expansion and the mechanism of acting on the remaining plants in the community were different from those of *T. heterospermus*. Nevertheless, the efficiency leading on to an almost complete elimination from the patch of all its original components was similar.

The first individuals of *C. arenaria* undoubtedly developed from generative diaspores. During a period favourable for germination the latter initiated the further, this time only vegetative, development of numerous polycormones, accumulated over a relatively small area. Noteworthy is the fairly concordant general direction and the similar growth rate of individual polycormones, due to which the sod did not grow from inside, but moved continuously in the same direction. This is probably associated with a stimulating effect of the allelopathic substances, produced by *C. arenaria*, upon the runners and shoots of its own individuals. According to this hypothesis an advantageous allelopathic effect would only be marked up to certain concentration levels of the active substances, which prevents excessive overcrowding of a population. It was probably for this reason that the rows of polycormones developed at similar distances from one another, as a result of which there was a regular spatial distribution of shoots. In competitively strong species such a distribution is particularly important for the undisturbed growth of individuals; many experimental investigations indicate that clump formation is only of advantage in the case of competitively weak plants which suffer less from their own density than when exposed to the action of competitively stronger plants (Zarzycki 1965, Mack and Harper 1977).

The proposition concerning the allelopathic properties of *C. arenaria*, or the influence of toxic substances from the decomposing remnants of its underground organs was proved by a mass dying of other plants which found themselves within the range of action of the sedge sod; a certain role was probably played by the competition for water. As revealed by the observation, the sequence of retreating of the individual species from the patch depended only on the distance from the “head” of the sod. Only a few of the *F. duriuscula* tussocks “engulfed” by the sod survived; others died, as did other plants of the community.

C. arenaria owed its success in the expansion also to the viability and longevity of its shoots. In the period lasting several years not even one out of the over two thousand vegetative shoots, produced then, died before attaining the old age. This type of survival of a population (Deevey Type I) is known to be peculiar to only a small number of all the plant species studied with respect to this, e.g., *Dactylorhiza incarnata* (L.) Verm., *D. sambucina* (L.) Verm., *Orchis mascula* L. (Tamm 1972).

The dominance period of *C. arenaria* is directly related to the life span of the individual polycormones, or — with reference to the same segment of space — to the life span of the individual shoots, for in no case was the sedge observed to colonize again areas left by the old retreating sod.

Festuca psammophila and *Koeleria glauca* represented dynamic population types different from those discussed earlier on. Both the rotation of individuals and changes in the seasonal and many years' abundance proceeded in them in a manner not noticeable at first sight. This is due to several properties, common to both species, as well as to the stage of development of their populations: (1) a long life cycle, (2) a low and only vegetative reproduction, (3) a low mortality, and (4) a balanced age structure of the population.

In the period preceding the research, the populations of the two species probably arose from seeds. This was indicated by the fairly regular spatial distribution of grass clumps within the *Festuco-Koelerietum glaucae* patches under study. The change of the mode of reproduction of the plants in the process of community succession probably resulted from changes in the competitive systems and the increasing death risk of the seedlings, which have a very low chance to develop freely in a thick growth of vegetation. A decline of the generative reproduction in dense phytocenoses is a frequent phenomenon in the kingdom of plants (Rabotnov 1960, Harper and White 1974, Falińska 1977).

The comparatively high resistance to the adverse changes in the biotope that the two species manifested at site 6, should be related mainly to the ability to store water in the rhizosphere, and to the extremely strongly developed root system. In direct contact with the grass tussocks, the *T. heterospermus* seedlings were unable to grow, because their taproots could not force their way through the interlaced grass roots forming one compact whole. The high percentage of grasses on site 7 (*F. duriuscula*, *F. psammophila* and *K. glauca*) should also account for the considerably lower efficiency of the expansion of *T. heterospermus* than on site 6.

The population dynamics of both annuals: *Androsace septentrionalis* and *Plantago indica*, was characterized first of all by great, fairly regular changes during the growing season: a fast growth in numbers during the germinating period, and an equally rapid decrease in the number of individuals still at the seedling stage.

The many years' variations in numbers of *A. septentrionalis* — against the percentage of dying individuals which was similar in all the years — were the function primarily of the number of seedlings. Thus a reduction in numbers, especially in the last 3 study years, indicated some adverse conditions, affecting the germination, and possibly the growth of the germs, as a result of the expansion of *T. heterospermus*.

Difficult to interpret is the highly variable, from year to year, population abundance of *P. indica*. Investigations have demonstrated that a fairly low percentage of the seeds in this species germinated; tests should, therefore, be made to experimentally determine the ability of the seeds to survive in the soil, and define the physical conditions essential to an efficient germinating. An abundant or very poor emergence of the seedlings in the individual years was probably the result of a joint action of many factors, favourable or adverse for the reproduction of this population.

A detailed discussion of the results relating to the populational phenomena will be included in the last part of the study (Symonides 1979b).

4. SUMMARY

The paper presents the most important results from investigations into the ecology of selected species and inland dune communities, carried out on loose psammophyte sods. The "loose sods" were communities with a cover of 40–60% in the first study year. On the basis of changes in the specific composition and numbers, per cent cover, frequency and biomass of populations of the individual species the inner dynamics and succession changes of the following communities were analysed: (1) Spergulo-Corynephorum in optimum phase of its development, (2) communities with *Carex arenaria*, (3) Festuco-Koelerietum glaucae – a facies with *Androsace septentrionalis*, (4) a typical variant of Festuco-Koelerietum glaucae, (5) Corispermum-Plantaginetum indiciae.

The following plant species, characteristic of the above communities and dominant in the patches considered were selected for detailed population studies: *Carex arenaria*, *Koeleria glauca*, *Festuca psammophila*, *Androsace septentrionalis*, *Tragopogon heterospermus* and *Plantago indica*. The scope of the population studies covered the assessment of the seasonal and many years' changes in density, spatial structure, composition of age and size, reproductiveness, mortality, net increase, and biomass production.

The investigations were carried out at permanent sites and plots in the Toruń Basin in the years 1968–1975. A detailed description of the methods, a sketch map of the study area, as well as the results relating to the initial stage of bare sand colonization, development of initial communities and of populational properties of *Corynephorus canescens* have been presented in the first part of the series (Symonides 1979a).

During the study period, the loose psammophyte sods showed a high dynamics and a large variety of changes.

As a result of the expansion of the *C. arenaria* population (Figs. 1, 3), there occurred significant changes in the specific composition of the patch of Spergulo-Corynephorum, and permanent changes in the biotope. Most of the species retreated under the pressure of the sedge sod, only a few of them being seen to colonize sands again after the withdrawal of the latter (Fig. 4). *C. arenaria* is probably capable of secreting allelopathic substances which are harmful to other plant species. The most important features of the population of this species are a regular spatial structure (Figs. 1, 2), and a great viability of juveniles and of generatively mature shoots; the population survival curve represents a Deevey Type I curve (Fig. 5).

In a Festuco-Koelerietum glaucae patch (site 6) a significant reduction in the floristic composition, and changes in abundance structure occurred as a result of a rapid expansion of *T. heterospermus* (Table II, Figs. 6, 7). In another patch of this association (site 7), in which an expansive growth of *T. heterospermus* population was prevented by a denser vegetation cover, the qualitative and quantitative structure of the vegetation did not undergo any significant transformations during the study period (Table III, Fig. 6).

The invasion of *T. heterospermus* (site 6) caused a considerable decrease in numbers in the *K. glauca* population, primarily due to a reduction in reproductiveness; the mortality varied only slightly from year to year. The reduction in reproductiveness was followed by changes in the age structure of the population: in the last study year senile tussocks represented almost 70% of the total number of individuals. In stabilized phytocenotic systems on site 7 no such changes could be seen in *K. glauca*. The most important results relating to *K. glauca* population have been presented in Figures 8–11. Figures 12–14 present the structure and dynamics of the population of *F. psammophila*, which, like *K. glauca*, reacted to the expansion of *T. heterospermus* by considerably reducing its numbers, and, like *K. glauca*, it showed a high stability on site 7.

In the expansive population of *T. heterospermus* unfavourable changes connected with overcrowding began at a relatively early stage: a retarded development of individuals, a reduction of their size and of diaspore production (Fig. 15). The dynamics of *T. heterospermus* was characterized by considerable seasonal variations connected with the emergence of large numbers of seedlings and their high mortality (Figs. 16, 17). Similar seasonal variations in numbers were seen in *A. septentrionalis* population (Fig. 18), multiplying (like *T. heterospermus*) only by seeds. Associated with the large numbers of seedlings emerging over a small area is not only their high mortality, but also a capability of plastic reactions of the survivors, as a response to the overcrowding pressure (Fig. 19), which was particularly strongly marked in *P. indica* (Fig. 20). Here, the mortality of the seedlings was not closely correlated with their density (Fig. 19), because of which the level of density of the adult individuals of *P. indica* was, in some plots, higher than in the populations of other plant species.

During the study period the population of *P. indica*, like most of the populations of the remainder of species in the Corispermo-Plantaginetum indicae patch, showed considerable variations in numbers (Table V, Fig. 19). The non-directional and irregular changes in the composition and quantitative structure of Corispermo-Plantaginetum indicae to a large extent resulted from the high (about 50%) proportion of annual and biennial species, and they indicate weak phytocenotic relations among the community components.

5. POLISH SUMMARY

W pracy przedstawiono najważniejsze wyniki badań luźnych muraw psammofilnych, dotyczące ekologii wybranych gatunków i zbiorowisk na wydmach śródlądowych. Jako „luźne murawy” potraktowano zbiorowiska o pokryciu 40–60% w pierwszym roku badań. Na podstawie zmian w składzie gatunkowym oraz liczebności, pokrywanu, frekwencji i biomasy populacji poszczególnych gatunków zanalizowano wewnętrzną dynamikę i sukcesyjne przemiany następujących zbiorowisk: 1) *Spergulo-Corynephorum* w optymalnej fazie rozwojowej, 2) zbiorowiska z *Carex arenaria*, 3) *Festuco-Koelerietum glaucae*, facja z *Androsace septentrionalis*, 4) *Festuco-Koelerietum glaucae*, wariant typowy, 5) *Corispermo-Plantaginetum indicae*.

Do szczegółowych badań populacyjnych wybrano gatunki roślin charakterystycznych dla wymienionych zbiorowisk i równocześnie dominujących w wytypowanych płatach: *Carex arenaria*, *Koeleria glauca*, *Festuca psammophila*, *Androsace septentrionalis*, *Tragopogon heterospermus* i *Plantago indica*. Zakres badań populacyjnych obejmował ocenę sezonowych i wieloletnich zmian zagęszczenia, struktury przestrzennej, struktury wieku i wielkości, rozrodzności, śmiertelności; przyrostu netto i produkcji biomasy.

Badania przeprowadzono w latach 1968–1975 w Kotlinie Toruńskiej, na stałych powierzchniach i poletkach. Szczegółowy opis metod, plan sytuacyjny powierzchni, a także wyniki badań dotyczące wstępnej fazy zasiedlania nących piasków, rozwoju inicjalnych zbiorowisk oraz populacyjnych właściwości *Corynephorus canescens* przedstawiono w pierwszej części pracy (Symonides 1979a).

Luźne murawy psammofilne wykazywały w okresie badań dużą dynamikę i dużą różnorodność zmian.

W efekcie ekspansji populacji *C. arenaria* (rys. 1, 3) nastąpiły istotne przekształcenia składu gatunkowego płatu *Spergulo-Corynephorum* i trwałe zmiany biotopu. Większość gatunków wycofała się pod naporem murawy turzycowej, przy czym tylko nieliczne ponownie zasiedliły piaski po jej ustąpieniu (rys. 4). Prawdopodobnie *C. arenaria* zdolna jest do wydzielania substancji allelopatycznych, szkodliwych dla innych gatunków roślin. Z najistotniejszych właściwości populacji tego gatunku wymienić można równomierną strukturę przestrzenną (rys. 1, 2) oraz dużą żywotność pędów juvenilnych i dojrzałych generatywnie; krzywa przeżywania populacji reprezentuje I typ krzywej Deevey'a (rys. 5).

Istotne zubożenie listy gatunków i zmiany w strukturze liczebności pomiędzy poszczególnymi komponentami zbiorowiska stwierdzono w płacie *Festuco-Koelerietum glaucae* (na powierzchni 6) pod wpływem gwałtownej ekspansji *T. heterospermus* (tab. II, rys. 6, 7). W drugim płacie tego zespołu (powierzchnia 7), w którym silniej zwarta pokrywa roślinna uniemożliwiła ekspansywny rozwój populacji *T. heterospermus*, jakościowa i ilościowa struktura roślinności nie uległy w okresie badań istotnym przekształceniom (tab. III, rys. 6).

W wyniku inwazji *T. heterospermus* (powierzchnia 6) znacznie zmniejszyła się liczebność populacji *K. glauca*, przede wszystkim w efekcie obniżonej rozrodzności; śmiertelność wahała się w poszczególnych latach nieznacznie. Wraz z obniżeniem rozrodzności zmianom uległa struktura wiekowa populacji: w ostatnim roku badań niemal 70% ogólnej liczby osobników stanowiły kępy senilne. Na powierzchni 7, w ustabilizowanych układach fitocenotycznych, nie stwierdzono podobnych zmian u *K. glauca*. Ważniejsze wyniki dotyczące populacji *K. glauca* zilustrowane są na rys. 8–11. Na rysunkach 12–14 przedstawiono strukturę i dynamikę populacji *F. psammophila*, która – podobnie jak *K. glauca* – zareagowała na ekspansję *T. heterospermus* znacznym obniżeniem liczebności i – podobnie jak *K. glauca* – wykazała dużą stabilizację na powierzchni 7.

W ekspansywnej populacji *T. heterospermus* dość wcześnie wystąpiły niekorzystne zmiany związane z przegęszczeniem: opóźniony rozwój osobników, spadek ich rozmiaru i produkcji diaspor (rys. 15). Dynamikę *T. heterospermus* charakteryzują duże zmiany sezonowe, związane z masowym pojawem siewek i ich wysoką śmiertelnością (rys. 16, 17). Podobne sezonowe wahania liczebności występują w populacji *A. septentrionalis* (rys. 18), pomnażającej się (tak jak *T. heterospermus*) wyłącznie z nasion. Z dużą liczbą siewek wyrastających na niewielkiej przestrzeni wiąże się nie tylko masowe ich wymieranie, ale także plastyczne reakcje przeżywających osobników jako reakcja na presję przegęszczenia (rys. 19), co szczególnie jaskrawo zaznaczyło się u *P. indica* (rys. 20). Śmiertelność siewek nie była tu ściśle skorelowana z ich zagęszczeniem (rys. 19), stąd też poziom zagęszczenia dorosłych osobników *P. indica* na niektórych poletkach był wyższy, niż w populacjach innych gatunków roślin.

Populacja *P. indica*, podobnie jak większość populacji pozostałych gatunków w płacie *Corispermum-Plantaginetum indicae* wykazywała w okresie badań duże wahania liczebności (tab. V, rys. 19). Niekierunkowe i nieregularne zmiany w składzie i strukturze ilościowej *Corispermum-Plantaginetum indicae* w znacznej mierze wynikają z dużego (ok. 50%) udziału gatunków jednorocznych i dwuletnich i świadczą o słabych związkach fitocenotycznych pomiędzy komponentami zbiorowiska.

6. REFERENCES

1. Ellenberg H. 1956 – Aufgaben und Methoden der Vegetationskunde. IV (In: H. Walter – Grundlagen der Vegetationsgliederung) – Eugen Ulmer, Stuttgart, 136 pp.
2. Falińska K. 1977 – Strategia i taktyka reprodukcyjna populacji roślinnych [Reproduction strategy and tactics of plant populations] – Wiad. ekol. 23: 229–257.
3. Gadgill M. 1971 – Dispersal: population consequences and evolution. – Ecology, 52: 253–261.
4. Grime J. P., Curtis A. V. 1976 – The interaction of drought and mineral nutrient stress in calcareous grassland – J. Ecol. 64: 975–988.
5. Harper J. L. 1977 – Population biology of plants – Academic Press, London-New York-San Francisco, 896 pp.
6. Harper J. L., White J. 1974 – The demography of plants – A. Rev. Ecol. Syst. 5: 419–463.
7. Jentys-Szaferowa J. 1959 – A graphical method of comparing the shapes of plants – Rev. Pol. Acad. Sci. 4: 9–38.
8. Krausch H.-D. von, 1968 – Die Sandtrockenrassen (*Sedo-Scleranthetea*) in Brandenburg – Mitt. flor.-soz. ArbGemein. (Rinteln), 13: 71–100.
9. Mack R., Harper J. L. 1977 – Interference in dune annuals: spatial pattern and neighbourhood effects – J. Ecol. 65: 345–363.
10. Rabortnov T. A. 1960 – O florističeskoj i cenotičeskoj peldočlennosti cenzov – Dokl. Akad. Nauk SSSR, 130: 671–673.
11. Rabortnov T. A. 1965 – O dinamičnosti struktury polidominantnych lugowych cenzov – Bot. Ž. 50: 1396–1408.
12. Salisbury E. J. 1942 – The reproductive capacity of plants. Studies in quantitative biology – G. Bell and Sons, London, 244 pp.
13. Salisbury E. J. 1952 – Downs and dunes – G. Bell and Sons, London, 304 pp.
14. Symonides E. 1974 – Populations of *Spergula vernalis* Willd. on dunes in the Toruń Basin – Ekol. pol. 22: 379–416.
15. Symonides E. 1977 – Mortality of seedlings in the natural psammophyte populations – Ekol. pol. 25: 635–651.
16. Symonides E. 1978 – Effect of population density on the phenological development of individuals of annual plant species – Ekol. pol. 26: 273–286.
17. Symonides E. 1979a – The structure and population dynamics of psammophytes on inland dunes. I. Populations of initial stages – Ekol. pol. 27: 3–37.
18. Symonides E. 1979b – The structure and population dynamics of psammophytes on inland dunes. IV. Population phenomena as a phytocenose-forming factor (a summing-up discussion) – Ekol. pol. 27: 259–281.
19. Tamam C. D. 1972 – Survival and flowering of some perennial herbs. II. The behaviour of some orchids on permanent plots – Oikos, 23: 23–28.
20. Vasilevič V. I. 1970 – Metod avtokorelacji pri izučeni dinamiki rastitelnosti – Trudy mosk. Obšč. Ispyt. Prir. 38: 17–23.
21. Whittaker R. M. 1973 – Handbook of vegetation science. V. Ordination and classification of communities – Dr W. Junk Publishers, The Hague, 737 pp.
22. Wilkoń-Michalska J. 1976 – Struktura i dynamika populacji *Salicornia patula* Duval-Jouve [Structure and dynamics of populations of *Salicornia patula* Duval-Jouve] – Uniwersytet Mikołaja Kopernika, Rozprawy, Toruń, 156 pp.
23. Wilkoń-Michalska J., Symonides E. 1974 – The influence of vegetation on the dynamics of soil humidity in the patch of *Spergulo-Corynephorum* Tx. (1928) Libb. (1933) – Fragn. flor. geobot. 20: 497–528.
24. Zarzycki K. 1965 – Obecny stan badań nad konkurencją (współzawodnictwem) roślin wyższych [The state of research on competition in higher plants]. I, II – Ekol. pol. B, 11: 107–123, 195–210.