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THE STRUCTURE AND POPULATION DYNAMICS OF PSAMMOPHYTES ON INLAND DUNES

III. POPULATIONS OF COMPACT PSAMMOPHYTE COMMUNITIES

ABSTRACT: Studies were carried out concerned with vegetation dynamics on fixed dune sands, and characteristics of the populations of three plant species: *Festuca duriuscula* L. (polycarpic, perennial), *Cerastium semidecandrum* L. (monocarpic, annual) and *Jasione montana* L. (monocarpic, biennial or perennial). During the study period lasting several years there occurred no significant changes in the qualitative and quantitative structure of the communities. Populations of the particular species showed a high stability of numbers over a many years' cycle, in spite of their different methods of reproduction and competitive power.

KEY WORDS: Inland dunes, psammophytes, populations of compact communities, population-size regulating mechanisms, density-dependent age structure, density-dependent size structure.

Contents

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1. INTRODUCTION

The present paper is the result of wider-scope studies concerned with the ecology of selected species and of selected psammophyte communities. The aim of the studies was to follow the changes subject to which are the structural and functional properties of the populations of individual species in the course of the formation and succession of plant communities, and to analyse the course and rate of dune overgrowing.

Field investigations were carried out, between March 1968 and end of July 1975, at 10 permanent sites representing different stages of dune overgrowing. A description of the area, soils, climate and vegetation can be found in the paper by Symonides (1974).

The formation and growth of the initial psammophyte communities of bare sands (sites 1–3), and the characteristics of the populations of *Corynephorus canescens* (L.) P. B., a pioneer plant of inland dunes, have been presented in the first part of this series (Symonides 1979a). The next part (Symonides 1979b) contains the most important results from studies carried out on loose sods on sands, that is, communities with a cover of 40–60%. It discusses: (1) vegetation changes in patches of Spergulo-Corynephoretum (Tx. 1928) Libb. 1933, Festuco-Koelerietum glaucae Klika 1931 (a facies with *Androsace septentrionalis* L. and a typical variant), Corispermo-Plantaginetum indicae Passarge 1957, and in a *Carex arenaria* L. community (sites 4–8); (2) properties of the populations of the characteristic and dominant plants in the above-named communities: *Carex arenaria*, *Koeleria glauca* (Schkuhr) DC., *Festuca psammophila* (Hackel) Krajina, *Tragopogon heterospermus* Schweigg., *Androsace septentrionalis*, and *Plantago indica* L.

The present, the third, part is concerned with the ecology of three plant species in communities compact in at least 80%, and with the dynamics of the vegetation on entirely fixed dune sands.

The investigations were carried out at two sites each of the size 16 x 16 m; site 9 represented a patch of the association Festuco-Koelerietum glaucae, a variant with *Festuca duriuscula*, site 10 – a skeleton community with *F. duriuscula* of a syntaxonomic grade not identified more closely.

Highly compact communities were few in number in the first study year, most often in the form of small-sized patches located within loose sods, representing the association Diantho-Armerietum Krausch 1959, or a community with *Festuca psammophila* and only a small admixture of other psammophyte species. The selection of the sites was influenced mainly by the large size of the biochore of the communities studied, and to a lesser extent by their floristic composition.

To examine the structure and dynamics of compact psammophyte communities, a census of species over an area of 256 m^2 was made 2–3 times a year, and an assessment of numbers, frequency, coverage and biomass of the populations of each of the components.

For detailed studies of the ecology of populations, three species, different in respect of their biology, were selected: *Festuca duriuscula* (a polycarpic perennial species), *Cerastium semidecandrum* (a monocarpic annual), and *Jasione montana* (a monocarpic biennial or perennial). An additional criterion taken into account during the selecting of species was the high level of their numbers, making it possible to obtain appropriately representative samples for statistical analyses; for this reason, *J. montana* was only examined at site 9.

The scope of the population studies included the estimation of seasonal and many years' variations in density, of the type of spatial structure, age structure, proportions of different growth-stage individuals, of the individual size composition, and of reproductiveness, mortality, net increment and biomass production.

The examinations were carried out primarily in permanent plots – in four replications for each species; the size of the plots – dependent on the size of the plants of each species – was: 4 m^2 for *F. duriuscula* and *J. montana*, and 1 m^2 for *C. semidecandrum*. Apart from the permanent plots, in 1969 at each of the two sites 100 young individuals of *F. duriuscula* (not present in the first study year) were selected to be used for an exact estimation of the rate of their growth and mortality at early life stages.

A detailed description of the methods, a map of the location of the sites, and a summarized description of weather conditions over the period 1968–1975 can be found in the first part of this series (Symonides 1979a).

2. RESULTS

2.1. THE STRUCTURE AND CHANGES OF THE VEGETATION IN FIXED DUNE SAND COMMUNITIES

Site 9. The vegetation of the patch represented a floristically rich association Festuco-Koelerietum glaucae. The phytocenose-forming species dominating in the patch in respect of numbers, coverage and biomass was *F. duriuscula* (Table I, Fig. 1). Tussocks of *F. duriuscula* formed distinct aggregations, usually regularly distributed on the site, each consisting of 8–14 tussocks; in an old bomb crater as many as 1607 compact small tussocks were aggregated over an area of only 24 m^2.

The population of *F. psammophila* was characterized by a fairly uniform spatial distribution of individuals: the remaining species formed a mosaic-like pattern of single species patches, characteristic of the sod vegetation of the dunes, the populations, except those of *C. semidecandrum* and *J. montana*, being characterized by a very low frequency: several per cent with a basic unit of 4 m^2. Other characteristics of the community included: (1) a high percentage of perennials and, except *F. duriuscula*, *F. psammophila* and *C. semidecandrum*, a low population abundance; (2) a rich – relative to other communities – set of associated species; (3) a patchy pattern of the populations of individual species, and (4) a complete absence of the moss and lichen layer, due to which, in spite of the considerable density of flowering plants (85%), over about 38% of the area bare sand could be seen.

In 1968, the total biomass of the vegetation (site 9) was estimated at about 66.5 kg. *F. psammophila* and *Thymus serpyllum* (Fig. 1) represented a considerable proportion in the biomass, in addition to *F. duriuscula*.

The species composition and the structure of numbers in the patch investigated underwent only slight changes during the study period (Table I). The community similarity index for the presence of species was, at the end of the seven-year period, 91.7%, and for abundance – 99.7% (Ellenberg 1956). It should also be emphasized that the turnover of individuals in the populations of perennial species was relatively low: 51.2% of the plants recorded on the site in the first study year persisted in the patch until 1975.

Although the stability of the system was high, certain data indicated significant, if slow, conversions in the phytocenose:

1. A complete retreat of *C. canescens* population which consisted only of mature or senile tussocks already at the beginning of the studies. The few seedlings recruited during the autumn of 1968 died, and in the subsequent years the population entirely lost its ability to reproduce.

Table 1. Species composition and numbers of the individual populations in the patch of the association Festuco-Koelerietum glaucae, a variant with *Festuca duriuscula*, at site 9
The syntaxonomic units were identified according to Krausch (1968)

Species	1968	1969	1970	1971	1972	1973	1974	1975
Character-taxa Koelerion glaucae								
Koeleria glauca	75	72	70	68	61	56	56	52
Festuca psammophila	1211	1214	1208	1207	1206	1199	1196	1091
Character-taxa Armerion elongatae								
Herniaria glabra L.	6	5	7	7	9	9	8	10
Armeria elongata (Hoffm.) Koch	121	124	174	188	205	215	219	222
Dianthus deltoides L.	0	0	0	5	7	11	14	27
Character-taxa Corynephorion								
Corynephorus canescens	41	39	35	18	0	0	0	0
Character-taxa Festuco-Sedetalia								
Thymus serpyllum L.	668	670	667	675	672	670	676	679
Cerastium semidecandrum	1470	1390	1486	1472	1468	1495	1470	1506
Character-taxa Sedo-Scleranthetea								
Trifolium arvense L.	211	178	236	315	249	275	215	246
Potentilla argentea L.	76	76	79	81	78	82	76	79
Arenaria serpyllifolia L.	111	98	126	211	174	136	185	174
Jasione montana	489	502	499	496	500	489	492	491
Rumex acetosella L.	27	35	42	26	39	41	41	37
Hieracium pilosella L.	67	85	113	96	85	89	92	81
Festuca duriuscula	4222	4276	4307	4349	4402	4489	4576	4691
Character-taxa Festuco–Brometea								
Centaurea rhenana Bor.	66	69	73	70	69	75	75	73
Potentilla arenaria Borkh.	37	49	48	47	48	43	45	44
Veronica spicata L.	17	14	13	14	14	12	10	13
Artemisia campestris L.	37	37	37	39	39	37	38	38
Dianthus carthusianorum L.	74	75	75	72	79	82	77	76
Euphorbia cyparissias L.	27	29	35	31	33	36	35	34
Other taxa								
Carex ericetorum Poll.	111	117	119	109	121	115	124	127
Galium verum L.	32	34	27	25	31	34	34	30
Knautia arvensis (L.) Coult	17	21	24	24	21	26	26	28
Hypericum perforatum L.	11	10	13	13	16	16	14	12
Chondrilla juncea L.	11	8	9	9	10	11	10	11
Peucedanum oreoselinum (L.) Moench	11	10	10	9	12	13	13	13
Carex hirta L.	8	8	7	7	8	6	8	7
Achillea millefolium L.	10	11	11	12	13	13	14	13
Bromus mollis L.	13	12	17	17	15	16	12	11
Scorzonera humilis L.	5	5	4	4	5	4	5	5
Carex caryophyllea Latourette	21	20	17	26	27	16	13	15
Calluna vulgaris (L.) Salisb.	4	4	4	4	5	5	4	4
Agrostis vulgaris With	9	8	8	9	9	10	11	12
Digitaria sanguinalis (L.) Scop.	0	0	0	0	0	0	2	16
Arabis arenosa (L.) Scop.	0	0	7	11	11	10	13	11
Total number of individuals	9316	9315	9707	9766	9741	9836	9899	9979

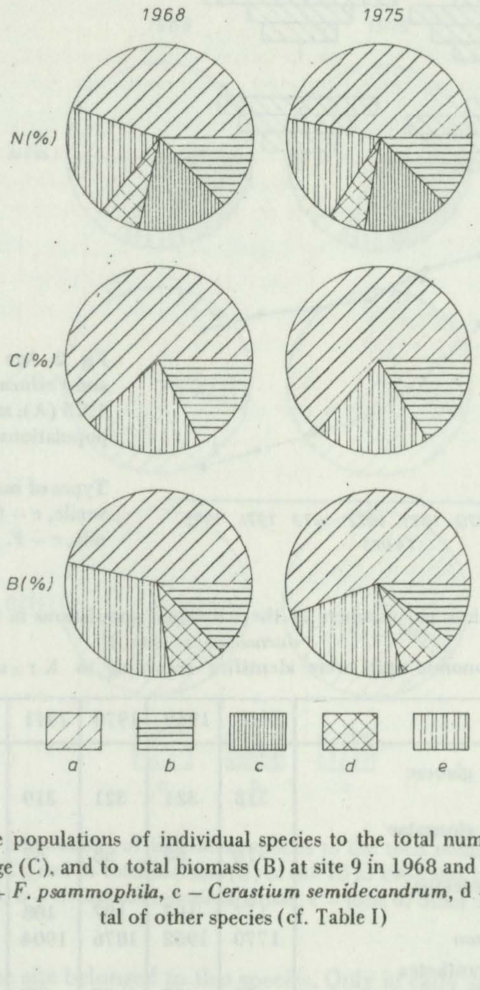

Fig. 1. Contribution of the populations of individual species to the total number of individuals (N), coverage (C), and to total biomass (B) at site 9 in 1968 and 1975

a – *Festuca duriuscula*, b – *F. psammophila*, c – *Cerastium semidecandrum*, d – *Thymus serpyllum*, e – total of other species (cf. Table I)

2. A gradual retreat of *K. glauca* and *F. psammophila* populations. The evidence to indicate the withdrawal of the populations of both species was first of all the changes in the age structure and general viability of the tussocks, and to a lesser extent a decrease in numbers (Table I, Fig. 2 A). The ageing process was particularly marked in the population of *K. glauca:* the proportion of old tussocks increased from year to year, and at the same time the fruiting fraction decreased (Fig. 2 B); in 1975, nearly all the *K. glauca* tussocks were dying.

3. A growth in numbers of the populations of the species characteristic of the Armerion elongatae alliance (Table I).

4. A growth in numbers and in the percentage in the total community biomass of the population of *F. duriuscula* (Fig. 1).

The overall surface cover was found to have increased by 5%, relative to the value recorded in 1968, and the biomass was found to have increased by 10.2 kg.

Site 10. The vegetation of the patch represented a floristically poor, strongly compact community with *F. duriuscula* (Table II). For the greater part of the year an average of 87.3%

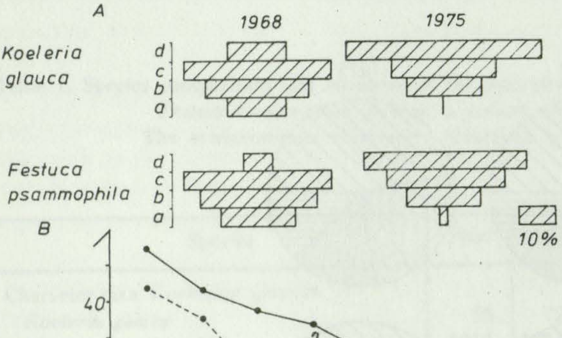

Fig. 2. Age spectrum of *Koeleria glauca* and *Festuca psammophila* in 1968 and 1975 (A), and the fruiting fraction of the populations compared during the studies (B) at site 9

Types of individual: a – this year's, b – juvenile, c – flowering and fruiting, d – senile, e – *F. psammophila*, f – *K. glauca*

Table II. Species composition and numbers of the individual populations in the community with *Festuca duriuscula* at site 10

The syntaxonomic units were identified according to Krausch (1968)

Species	1968	1969	1970	1971	1972	1973	1974	1975
Character-taxa Koelerion glaucae								
Festuca psammophila	318	321	321	319	318	309	309	307
Character-taxa Armerion elongatae								
Armeria elongata	76	68	68	67	64	64	63	62
Character-taxa Festuco-Sedetalia								
Thymus serpyllum	117	107	107	108	105	105	104	102
Cerastium semidecandrum	1770	1952	1876	1904	1852	1796	1839	1888
Character-taxa Sedo-Scleranthetea								
Trifolium arvense	39	42	27	36	35	45	21	19
Potentilla argentea	21	17	16	14	11	11	10	7
Jasione montana	21	28	36	35	33	33	32	28
Festuca duriuscula	5820	5824	5832	5832	5830	5836	5839	5847
Character-taxa Festuco-Brometea								
Centaurea rhenana	27	26	25	25	22	22	21	20
Potentilla arenaria	111	112	112	109	109	107	107	102
Veronica spicata	11	11	17	16	10	9	9	11
Dianthus carthusianorum	17	26	25	16	16	17	15	17
Other taxa								
Knautia arvensis	11	11	13	10	12	12	11	12
Chondrilla juncea	7	6	7	7	8	8	8	9
Carex hirta	17	10	12	12	14	16	13	14
Bromus mollis	61	58	58	76	61	85	56	49
Agrostis vulgaris	11	13	21	26	27	26	29	32
Total number of individuals	8455	8632	8573	8612	8527	8501	8486	8526

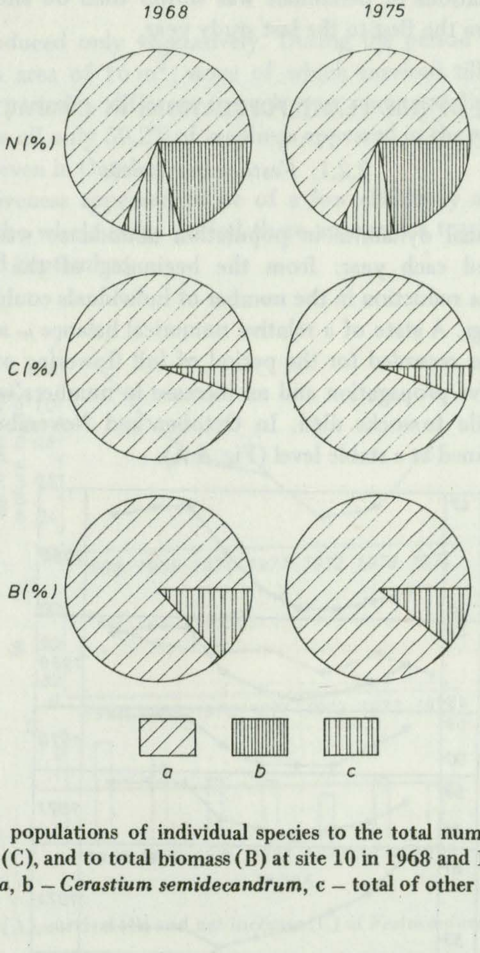

Fig. 3. Contribution of the populations of individual species to the total number of individuals (N), coverage (C), and to total biomass (B) at site 10 in 1968 and 1975
a – *Festuca duriuscula*, b – *Cerastium semidecandrum*, c – total of other species (cf. Table II)

of all the vegetation on the site belonged to this species. Only in early spring was the proportion of *F. duriuscula* smaller due to the mass appearance of *C. semidecandrum* individuals, but even then it amounted to about 68% of the total number of plants in the patch. The dominance of *F. duriuscula* was strongly marked, both in respect of numbers, coverage and total biomass (Fig. 3).

F. duriuscula clones, clearly separated from one another, uniformly colonized the whole area; each consisted of 7–16 tussocks. Individuals of other species occurred each year with a very low frequency, only in several to between ten and twenty aggregations, as a rule single-specific. As at site 9, the community was devoid of the moss and lichen layer.

During the period of study, no changes were observed in the species composition of the phytocenose, and the total number of plants in the patch, and the abundance of the populations of the particular species varied only slightly from year to year (Table II). The cover of the surface did not change, and there was only a slight increase in the total plant biomass: from 72.5 kg in 1968 to 76.6 kg in 1975; throughout the study period *F. duriuscula* tussocks represented 87–90% of the total biomass (Fig. 3). Thus all changes in the community were exclusively connected with the inner dynamics of the phytocenose, whereas the turnover of individuals in the populations of perennials was slower than on site 9: 66.5% of individuals survived in the patch from the first to the last study year.

2.2. CHARACTERISTICS OF THE PLANT POPULATIONS IN COMPACT PSAMMOPHYTE SODS

2.2.1. *Festuca duriuscula*

Site 9. The seasonal dynamics in population abundance was characterized by small, regular changes repeated each year: from the beginning of the growing season to June (sometimes until July), a reduction in the number of individuals could be seen due primarily to the mortality of seedlings. A state of a relative numerical balance – at the level of the seasonal minimum density – was recorded for the period of full flowering of the tussocks. In August and September, vegetative propagation and an increase in numbers were observed, although at the same time the senile tussocks died. In October and November the abundance of the population usually remained at a stable level (Fig. 4 A).

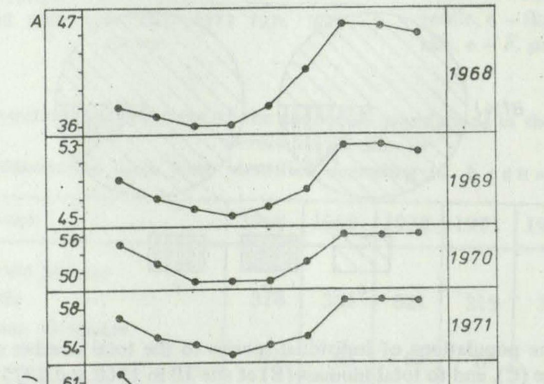

Fig. 4. Seasonal (A) and many years' (B) abundance dynamics of *Festuca duriuscula* population at site 9

In the many years' abundance dynamics an increase in the number of individuals was recorded for the years 1968–1970, and then a state of a complete equilibrium (Fig. 4 B, Table I).

The population reproduced only vegetatively. During the period of several years only 72 seedlings appeared in an area of 16 m^2, none of which survived till the end of the growing season. The germinating period – different in each year – was not directly connected with the weather conditions. All in all only 59.2% of seedlings appeared in the spring, the remainder – in August, September, and even in October.

Vegetative reproductiveness appeared to be of a low efficiency and variable from year to year (Fig. 5 A). During the whole study period there appeared a total of 244 tussocks, mainly at the turn of August and September.

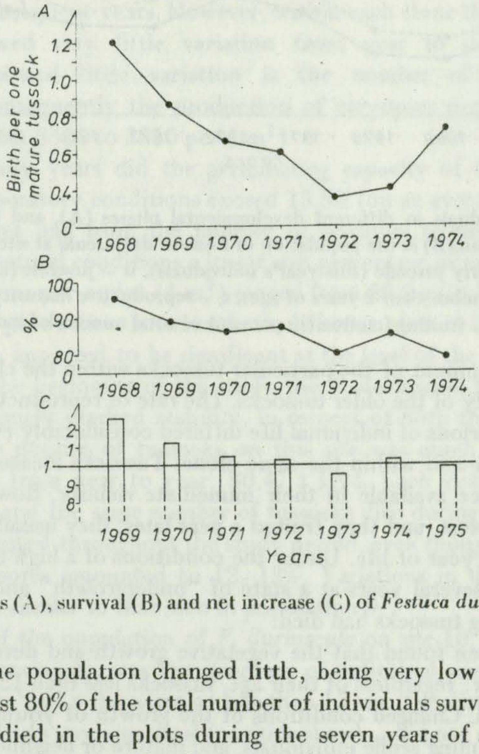

Fig. 5. Reproductiveness (A), survival (B) and net increase (C) of *Festuca duriuscula* population at site 9

The mortality of the population changed little, being very low throughout the period of study. Each year at least 80% of the total number of individuals survived (Fig. 5 B). Among the 184 individuals which died in the plots during the seven years of study the prevailing stages were seedlings (39.1%) and senile individuals (23.9%); the contribution of this year's vegetative propagules, juvenile and mature tussocks was 17.4, 13.1, and 6.5%, respectively. The death risk of *F. duriuscula* was thus the highest at the early life stages, and it clearly decreased during the period of reproductive maturity.

The very low mortality, observed in the first four study years, resulted in a positive net increase of the population (Fig. 5 C), in spite of a reduction in the reproductiveness; in the second half of the study period the value of the net increase coefficient – approaching unity – indicated a stabilized level of numbers in the population.

In the plots, the spatial structure of the population was characterized by a highly aggregative nature of the distribution, associated primarily with the type of reproduction. The same number of aggregations (clones) persisted for several years, the variation in the number of tussocks being similar each year. However, the percentages of juvenile, reproductively mature, and senile individuals in the population were subject to a fairly high variation (Fig. 6 A).

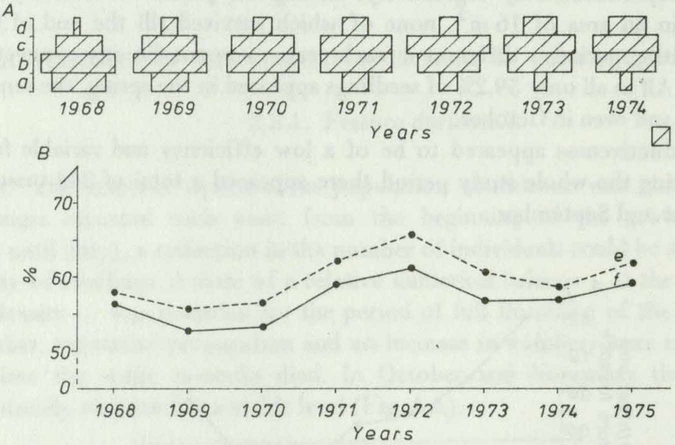

Fig. 6. Percentages of individuals in different developmental phases (A), and the flowering and fruiting fraction (B) in the population of *Festuca duriuscula* at site 9

Developmental phases: a – early juvenile (this year's individuals), b – juvenile (non-reproducing individuals in the second year of life, or more than 2 years of age), c – reproductive maturity, d – senile; e – flowering fraction, f – fruiting fraction (in per cent of total number of individuals)

The growth and development of the particular tussocks within the clones depended on their location and on the viability of the older tussocks. The rate of reproductive maturation, and the length of the successive periods of individual life differed considerably even between individuals produced in the same year and within the same clone. Tussocks located outside clones with a sufficiently large free space available in their immediate vicinity, flowered in the second, or third year of life at the latest, and they fruited a year later; they usually attained reproductive maturity also in the third year of life. Under the conditions of a high tussock density, juvenile individuals remained for several years at a state of "undergrowth" and they usually flowered only after the neighbouring tussocks had died.

Furthermore, it has been found that the vegetative growth and development of individuals are closely linked together: regardless of their age, tussocks less than 13 cm in diameter did not produce generative shoots. Changed conditions of the growth of young tussocks, as a result of the death of the overwhelming senile individuals, and mature or neighbouring "sister" tussocks, caused in the first place a fast increase in the vegetative biomass, and only then the production of the first panicles.

The dependence of the growth and development rates of young individuals on the density of clones caused considerable differences in the length of the juvenile phase between individuals: from two to over seven years. Of the hundred individuals selected for detailed observations of the rate of their development only 7 flowered in 1971, and in the following years – 13, 16, 7 and 8. Up to the end of the studies 19 tussocks died, and 30 persisted in the juvenile stage, being small tussocks 7–11 cm in diameter. Tussocks which were the first to flower began to die already in the last year, and did not produce generative shoots; the remaining tussocks flowered every year, although they did not fruit every year. The fruiting fraction of *F. duriuscula* population was thus smaller than the flowering fraction (Fig. 6 B). The observations have shown that the length of the reproductive and senile phases is subject to the same variations as is the juvenile phase.

The age of the particular tussocks of *F. duriuscula* cannot be inferred from their diameter, nor from the number of generative shoots. The latter is subject to considerable variations – from 2 to 37 panicles per tussock – regardless of the age, size (above the minimum diameter of about 13 cm) and the ecological situation of the tussock. It appears, therefore, that although the attainment of generative maturity depends primarily on the attainment of an appropriate vegetative biomass by each juvenile individual, the intensity of flowering (and of fruiting) does not show such dependence. An exception was the relatively young tussocks which produced in the first flowering year no more than 2–3 panicles with a small (2.27 ± 0.26) number of caryopses in an average infructescence; older tussocks, even though they flowered for the first time, produced a large and highly variable number of generative shoots in the first year of their fruiting, and in the subsequent years. However, within each clone the joint number of panicles characteristically showed very little variation from year to year. Another character in *F. duriuscula* that showed little variation is the number of caryopses in an average infructescence, and consequently the production of caryopses per unit area revealed a small range of variation – from 3560 to 3850 per 4 m^2.

In none of the study years did the germinating capacity of the generative diaspores of *F. duriuscula* under laboratory conditions exceed 13.5% (on an average 12.25 ± 0.8%); from the production of diaspores and from the number of seedlings recruited in the plots it can be concluded that under natural conditions a lower still percentage of caryopses germinate.

Biomass production as per a plot (4 m^2) ranged from 88.8 g (in 1968) to 127.8 g (in 1971); differences in biomass production between both different plots in the same year, and different years in the same plot, appeared to be significant at the level of the adopted risk of error (5%).

Site 10. From the beginning of the study the *F. duriuscula* population on this site was characterized by a strongly marked stability, in respect of both the structure and abundance dynamics. The average density of tussocks on this site was much higher than on site 9, and insignificantly variable from year to year: 80.47 ± 1.94. Each year 8–11 new tussocks were recruited in the plots, and the same number of tussocks died during the year. No seedlings, not even a single one, appeared throughout the study period, even though the germinating capacity of the generative diaspores amounted to 12–13%. Variations in density during the growing season showed a course similar to that seen in population 9.

A specific feature of the population of *F. duriuscula* on site 10, different from that of the population discussed previously, was the structure of individual size (tussock diameter): on an average 80% of tussocks had a diameter of less than 13 cm. The distribution of individual sizes in the population – clearly asymmetrical (positive-skew) – did not differ significantly between the particular years (Fig. 7).

The predominance of small tussocks in the population was the basic cause of the small differences in the coverage of site 10 – relative to site 9 – in spite of the high level of numbers in population 10.

As in population 9, only tussocks of appropriate size (more than 13 cm in diameter) flowered and fruited; thus the flowering and fruiting fraction in this population was very small, being three times lower than that of the formerly-discussed population. The number of panicles in an average fruiting tussock was 29 ± 6.5, whereas the number of caryopses in one panicle – 11.85 ± 0.65; the latter character did not differ between tussocks or years.

The development of *F. duriuscula* individuals was very slow: of the 100 young tussocks recruited during 1969 only 13 attained the flowering phase before the end of the research; 11 individuals died, while the remaining ones survived until 1975 as small juvenile individuals.

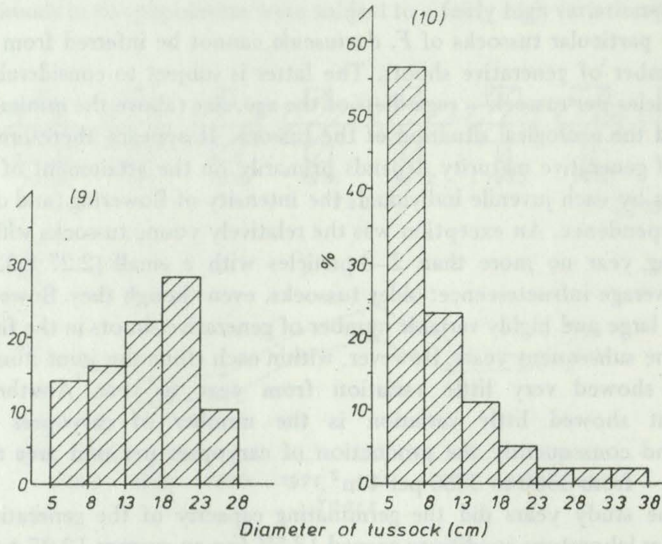

Fig. 7. Proportions of different-sized (diameter of tussocks – always measured during the flowering period) in *Festuca duriuscula* populations at sites 9 and 10 (average values for 8 years)

Biomass production in the population – relatively low and not differing much in the particular years – ranged from 92.6 to 98.8 g of dry weight as calculated per plot surface area.

Due to the relatively short study period, the long life history of *F. duriuscula*, and the great individual variation in respect of the rate of the phenological growth, it was impossible to work out the survivorship curve of the population, or to determine the life span of an average individual.

2.2.2. *Cerastium semidecandrum*

In both the compact sod patches under study the population of *C. semidecandrum* was characterized by a high stability of numbers over the many years' cycle; each year they colonized almost the same gaps between grass tussocks. At site 10 the population frequency was greater by 6% than at site 9, but the average real density per 1 m^2 did not differ significantly. Moreover, a detailed study carried out in the plots of both sites has demonstrated that from the statistical point of view the structure and function indices examined in the populations compared did not differ significantly; the results – presented only for the population at site 9 – apply equally also to that at site 10.

The abundance of *C. semidecandrum* population showed considerable, regular changes during the growing season. Each year the population attained the maximum density level on the fourth or sixth day from the beginning of germination, and 2–3 days later a rapid fall was already seen: about 60% of the individuals died in the seedling phase, and about 25% in the vegetative growth phase. It was at the time of flower bud formation that the mortality of the population was clearly decreasing, and during the flowering and fruiting periods only single

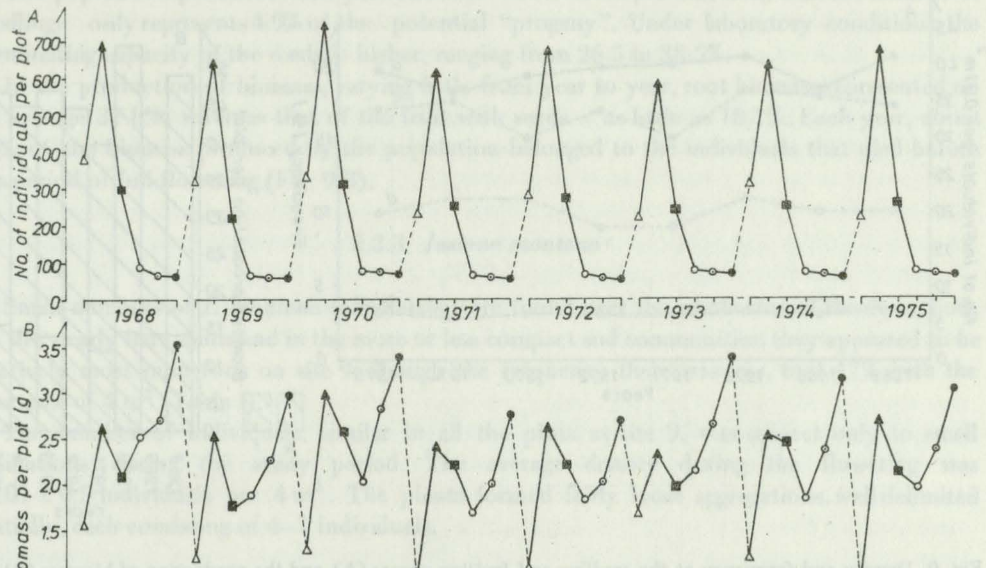

Fig. 8. Seasonal and many years' dynamics of numbers (A) and biomass (B) in *Cerastium semidecandrum* population at site 9

Phenological phases: a – beginning of germination, b – full germination, c – beginning of vegetative growth, d – budding, e – flowering, f – fruiting

individuals were dying (Fig. 8 A). Each year the total number of individuals that survived represented as small a proportion as 10.06 ± 1.7%.

Because of the short period of seed germination and establishing of seedlings, the value of the maximum population density of *C. semidecandrum* was at the same time a measure of the total number of seedlings recruited per unit area.

As a result of the high mortality of the individuals in early developmental stages, the biomass state curve of the population in the growing season has two distinct peaks, with the depression corresponding to the period of mass mortality of seedlings, in some years extending over the beginning of the vegetative growth period (Fig. 8 B).

The whole life cycle of *C. semidecandrum* is completed within 34–44 days, being the shorter, the later the first seeds germinate. The dates of flowering and fruiting in the individual years were similar, although the date of the beginning of germination in the extreme case differed by two weeks (cf. Symonides 1978).

The spatial structure of the population was characterized by a high degree of aggregation, within both the biochore and the plots. In the plots, with a base unit of 0.01 m^2, the frequency did not exceed the value of between ten and twenty per cent, even during the seasonal maximum density (Fig. 9 A). As a result of the dying of singly growing seedlings, during the flowering period the frequency dropped to 8–11%. The average density of the population in

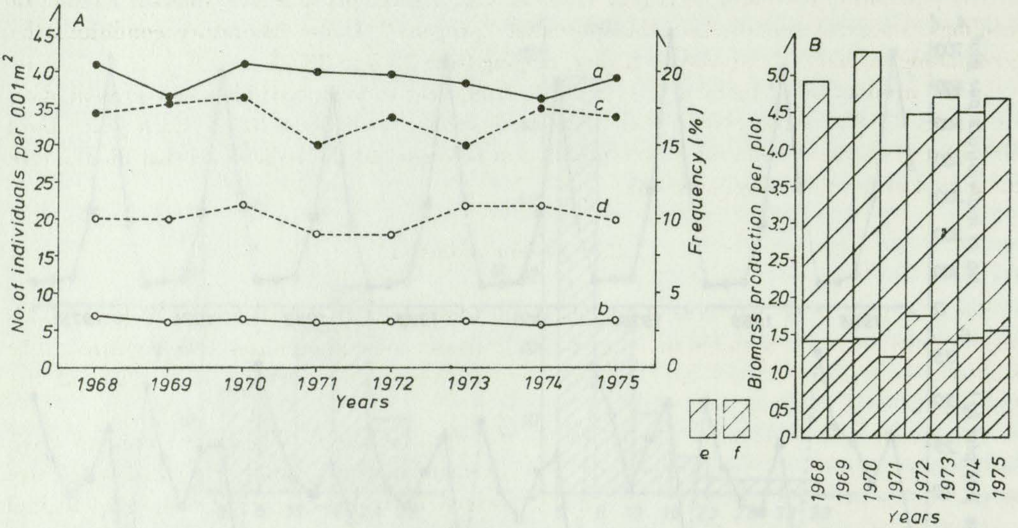

Fig. 9. Density and frequency at the seedling and fruiting phases (A), and the production of biomass (B) by *Cerastium semidecandrum* population at site 9
a – seedling density, b – density of fruiting individuals, c – seedling frequency, d – frequency of fruiting individuals; e – proportion of production by individuals which survived till flowering, f – proportion of production by individuals that died before flowering

analogous phenological phases of the individuals was maintained at a similar level throughout the study period, although the individual aggregations in the plots differed rather considerably from one another in respect of the number of individuals (Fig. 9 A).

The density at which the plants of *C. semidecandrum* grew, had a significant effect on their final size: the correlation coefficients for the number of individuals per unit area, and the average size of an individual in that area ranged from $r = -0.89$ to $r = -0.91$. As a result of this relationship, the distribution of various-sized individuals in the population was characterized by a clear asymmetry, the fraction of individuals of the same size class, and the number of classes in the individual years being similar. No statistically significant differences (even at the 1% level of error risk) in individual size (height) were found during the study period (Fig. 10).

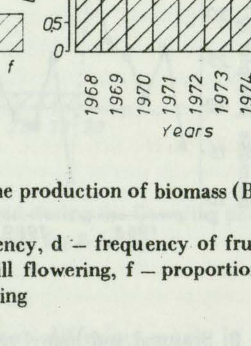

Fig. 10. Percentage of flowering individuals of different sizes (height) in the population of *Cerastium semidecandrum* at site 9 (average values for 8 years)

The flowering and fruiting fraction corresponded to the fraction of the individuals which survived until that phase. An average plant produced 13.4 ± 1.2 flowers, only 58.8 ±0.7% of which developed to produce seed-filled capsules. Seeds varied considerably in number from fruit to fruit (from several up to thirty odd), irrespective of the size of the individuals and the density at which they grew. Thus density had no significant effect on the reproduction of *C. semidecandrum:* individual diaspore production was similar in both the very small individuals and the sizeable ones.

The population produced each year 12017.5 ± 27.7 seeds per unit area; thus the number of seedlings only represents 4.9% of the potential "progeny". Under laboratory conditions the germinating capacity of the seeds is higher, ranging from 26.5 to 38.5%.

In the production of biomass, varying little from year to year, root biomass represented on an average 37.8%, whereas that of the fruit with seeds – as little as 18.7%. Each year, about 30% of the biomass produced by the population belonged to the individuals that died before the period of full flowering (Fig. 9 B).

2.2.3. *Jasione montana*[*].

Small numbers of *J. montana* individuals were found over the whole area of the dune, both on the nearly bare sands and in the more or less compact sod communities; they appeared to be relatively most numerous on site 9, though the frequency there was low, too: 17% with the base unit of 4 m² (Table I).

The number of individuals, similar in all the plots at site 9, was subject only to small oscillations during the study period. The average density during the flowering was 29.01 ± 0.5 individuals per 4 m². The plants formed fairly loose aggregations, well delimited spatially, each consisting of 4–7 individuals.

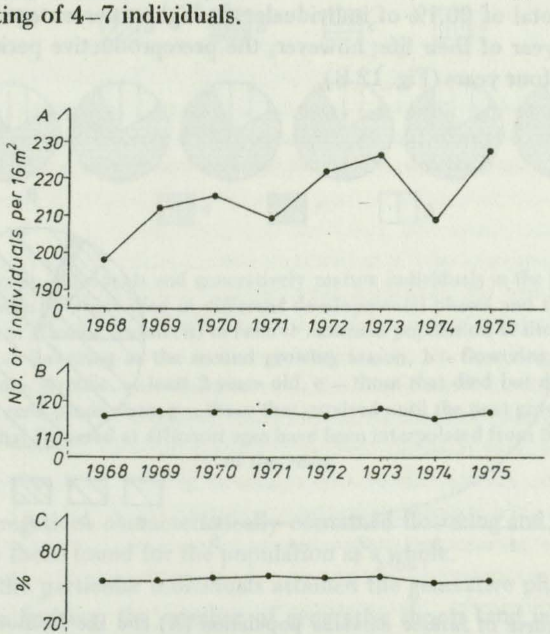

Fig. 11. Numbers of seedlings (A), flowering individuals (B), mortality (C), and net increase (D) in *Jasione montana* population at site 9

The maximum density of the population was attained during the germination and seedling establishing, which in essence takes place in the spring and lasts 2–3 months; small numbers of seedlings which in some years appeared also at the turn of August and September died already after two weeks.

Each year a similar joint total number of seedlings appeared in the plots, on the average 214.7 ± 9.9 (Fig. 11 A). In the full-flowering period (July) the abundance of the population was lower by almost a half than during the seasonal maximum, and almost identical in the different years (Fig. 11 B). Regardless of the weather conditions, the fractions of dying individuals of the population, found in the different years, were almost identical (Fig. 11 C), so the net increase coefficient was always approaching unity (Fig. 11 D).

The mortality of the population was the highest in the seedling phase. Each year 78.7 ± 1.3% individuals died already in the first 2–3 weeks of their life. In the later phases the death risk was much lower. Moreover, the survivorship curve of *J. montana* population (Fig. 12 A) shows that the total life span of the population was more than two years, although *J. montana* is in essence a plant whose life history is completed within two growing seasons. On an average 6.8 ± 0.8% of individuals of one pool of seedlings survived till the third year of their life, 2.1 ± 0.9% till the fourth, and 0.48 ± 0.03% till the fifth growing season. The generative phases were attained by a total of 20.1% of individuals; the highest percentage of individuals attained them in the second year of their life; however, the prereproductive period of some individuals was extended to last four years (Fig. 12 B).

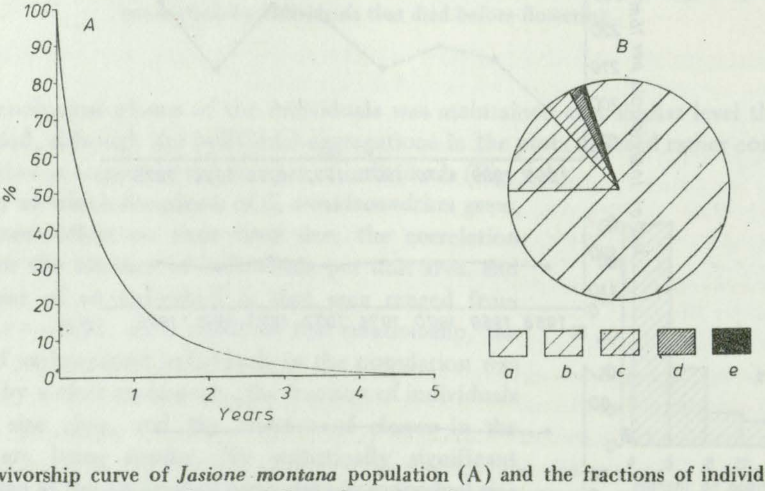

Fig. 12. Survivorship curve of *Jasione montana* population (A) and the fractions of individuals that died before attaining the generative phase and those that attained generative maturity in successive years of their life (B) (average values for the study period) at site 9

a – fraction of individuals which died before attaining the generative phase, b–e – fractions of individuals which attained generative maturity – in the second, third, fourth and fifth life year, respectively

The development rate of the individual plants was fairly tightly linked with the rate of their vegetative growth in the first life year: the first to flower were the plants which attained the largest rosette size; small-sized individuals, with a small number of leaves in the rosette, did not produce generative shoots in the next (the second) growing season, and as juvenile forms they lived then a longer time. The average life span of an individual in the population was only 7.5 months.

The plants died after seed production, irrespective of the duration of the juvenile phase. In *J. montana* the senile period does not practically exist; at the time of ripening of the last fruit almost the whole plant is withered. For this reason, two groups of individuals, at the most, can be distinguished in a population as regards their developmental phase: juvenile, and those reproductively mature. However, each of the two groups consists of different-aged individuals (Fig. 13 A). Figure 13 A shows that the percentage of reproducing individuals in the population only slightly varied from year to year; the proportion of plants flowering in the second year of life and in the subsequent years was subject to greater variations. Noteworthy is the fact that the range of variation of the number of flowering individuals in four plots was small – from 41 to 45. In the juvenile group the quantitative relations between this year's and "retarded" individuals did not undergo significant variations in the study years compared.

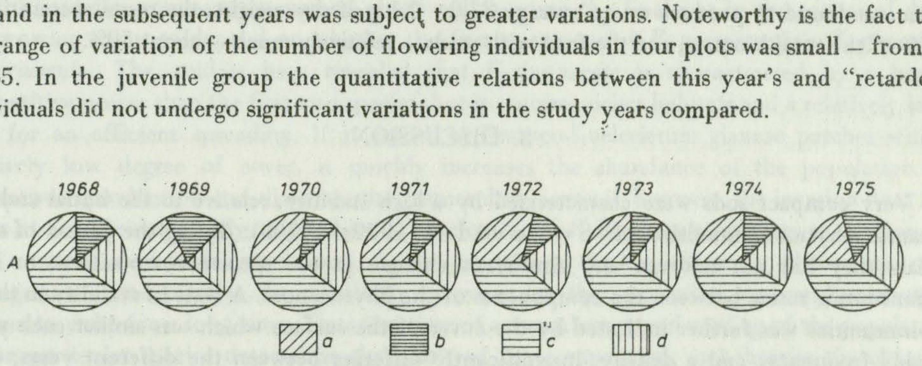

Fig. 13. Fraction of juvenile individuals and generatively mature individuals in the full-flowering period (A), and the fraction of individuals which died in different developmental phases and those that survived till the next growing season (B) in *Jasione montana* population at site 9

Types of individual: a – flowering in the second growing season, b – flowering, more than 2 years old, c – this year's juvenile, d – juvenile, at least 2 years old, e – those that died but developed from this year's seedlings, f – dead after seed production, g – those that survived until the next growing season; for 1968 the fractions of individuals that flowered at different ages have been interpolated from the data for the remainder of the years

The individual aggregations characteristically contained flowering and juvenile individuals in proportions similar to those found for the population as a whole.

The age at which the particular individuals attained the generative phases had no effect on the abundance of the fruiting; the number of generative shoots (and infructescences) ranged from 1 to 17 and it differed even between individuals of the same age. Nevertheless, the total number of infructescences produced by the population per unit area was each year similar, amounting to 294 ± 4.5 per 4 m^2.

The flowering and fruiting periods of individual plants lasted 2–3 months. The generative shoots did not grow simultaneously during the growing season, the first and the last one usually producing smaller infructescences with a much smaller number of seeds.

Seed production by *J. montana* population is very high: it amounts to about 2500 seeds per an individual, and about 7500 per 1 m^2. The seeds are small (0.1–0.2 mm in length) and they have a low germinating capacity: in Petri dishes under laboratory conditions on the average only 1.1% of seeds germinated. Assuming that seeds are not carried out of the site by the wind, it was estimated that under natural conditions about 0.17% germinated. Thus the reproductiveness of the population was very low.

Another expression of stability of the *J. montana* population was the similar "mortality structure": seedlings and individuals which had produced seeds always represented similar percentages among the dead individuals (Fig. 13 B). Of the plants that survived until the second year 97.5% attained generative maturity.

The production of biomass did not significantly vary during the study period. The population was found to produce on an average 37.8 + 2.1 g of dry weight, the roots accounting for 27% of the total biomass, and the fruit with seeds – relatively much – about 50%.

3. DISCUSSION

Very compact sods were characterized by a high stability, relative to the initial and loose psammophyte communities (cf. Symonides 1979a, 1979b): during the period of several years they did not undergo any significant changes in the species composition, or in the quantitative ratios between the components of the phytocenose. A state of stability in the two communities was further indicated by the cover of the surface which was similar each year, a stable frequency, and a density, insignificantly differing between the different years, of the populations of most species, as well as a similar level of total biomass. Thus the changes that were taking place in the phytocenoses consisted mainly in a renewal of the composition of individuals in the populations of the particular species.

Of the two patches selected for investigations into the dynamics of compact psammophyte communities only site 9 showed certain tendencies towards directional changes in the vegetation. The retreat from the patch of the population of *Corynephorus canescens*, the decreased viability and numbers of the characteristic species of the Koelerion glaucae alliance, and at the same time a permanent increase, though a slow one, in numbers of the populations of the species characteristic of the Armerion elongatae alliance indicate that the patch under study represented the association Festuco-Koelerietum glaucae in its terminal phase, while the direction of the succession was, most likely, towards the association Diantho-Armerietum Krausch 1959 (Armerio-Festucetum Knapp 1941). However, the steadily growing abundance of the population of *Festuca duriuscula* suggests the possibility of a different course of succession, as a result of which Festuco-Koelerietum glaucae will be replaced by a floristically poor community consisting mainly of *F. duriuscula* tussocks.

The *F. duriuscula* patch at site 10 – with the highest density among the sods under study – had all the features characteristic of a durable, fully stabilized community. This does not mean, however, that communities of this type represent the only end links in a succession series of sod psammophyte communities. It can be concluded from the observation that it is possible to include among the parallel, relatively stable communities also patches of Festuco-Koelerietum glaucae with a high degree of cover and a large percentage of the species whose names are contained in the name of the association, as also communities made up almost exclusively of *Festuca psammophila* tussocks, only with a small admixture of other species. Durable in their nature may probably be also Diantho-Armerietum patches, provided *F. duriuscula*, a competitively strong species, does not spread in them at an earlier stage.

It should be pointed out that the geographical position of the study area, and the transitional climate associated with it (cf. Ziembińska 1969) make possible the development of patches of both the subcontinental association Festuco-Koelerietum glaucae and the Diantho-Armerietum association; in the latter association a predominance is marked of the species whose centre of distribution is in central and western Europe (Kornaś 1972). In both cases, in the study area there form phytocenoses poorer in species than the typical associations described in the relevant literature (Celiński 1953, Piotrowska and Celiński 1965, Radomski and Jasnowska 1965, Fijałkowski 1966, Piotrowska 1966, Ceynowa 1968, Fijałkowski and Górski 1968, Celiński and Balcerkiewicz 1973 and others).

Which of the communities named above will become the final one in the course of dune overgrowing seems to depend on whether the first to encroach is *F. psammophila*, *K. glauca* or *F. duriuscula*. The studies have revealed that *F. duriuscula* is characterized by a higher competitive power than the first two species, but it requires richer habitats and a relatively large area for an efficient spreading. If it settles in Festuco-Koelerietum glaucae patches with a relatively low degree of cover, it quickly increases the abundance of the population by generative reproduction and displaces the former dominants; if, however, the invasion does not occur at a sufficiently early stage, there is no chance for *F. duriuscula* seedlings to develop. In such a case *F. duriuscula* spreads very slowly, because of the low efficiency of the vegetative propagation. Consequently, the possibility increases for the association Festuco-Koelerietum glaucae to exist for a long time. Thus the time of encroachment and settling of the population of the particular species determines the result of the competition, and thereby the ultimate result of the succession changes in the psammophyte communities (cf. Gadgill 1971).

The stability of the composition and structure of the compact communities indicates a state of "fullness" of the phytocenose, as a result of its having been filled with the particular biotypes (Rabotnov 1969), and a complete utilization of the available niches (cf. Mc Naughton and Wolf 1970). Noteworthy is the fact that in stabilized systems the populations of each of the species are characterized by a considerable equilibrium of the balance of numbers, in spite of the different ways of their reproduction, considerable differences in the coefficients of reproductiveness and mortality, and different dynamic values. The dominance of *F. duriuscula* in compact psammophyte communities shows that by contrast to other species it is better adapted to the utilization of the supplies of the habitat under conditions where there is pressure exerted by the organisms belonging to other species. According to Hutchinson (1965) and McNaughton and Wolf (1970) the dominant species are adapted to a much larger number of dimensions in their *n*-dimensional niches, and consequently they less often encounter factors limiting their free growth and development. It must be pointed out here that the dominance of *F. duriuscula* concerned both its quantitative predominance and predominance in the coverage and biomass, that is, in all the indices used for the distinguishing of dominants in plant communities (cf. Chadwick and Dalke 1965, Whittaker 1965, McNaughton 1968). The remaining species, "limited" by the competitive action of the dominant, have a much smaller real niche, relative to the potential possibilities of utilizing a "maximum-niche" (Hutchinson 1965).

F. duriuscula owes its large competitive potential and dominance to its strongly developed system of roots which penetrate a considerable volume of soil to utilize the water and mineral compounds contained in it; the root weight to the above-ground parts' weight ratio is much larger in *F. duriuscula* than in *F. psammophila* or *K. glauca* (Darowicka 1974). Growing closely together, the roots form a compact mass which makes it difficult for the plants of other species to penetrate. It must also be emphasized that owing to their capability to retain water in the rhizosphere, the roots of *F. duriuscula* cause an overdrying of the soil in their immediate surroundings, which additionally affects the free growth and development of the plants without this ability.

Although the possibility to "defend" their own individual territory gives the tussocks of *F. duriuscula* the chance to win in the competitive systems, the compact mass of roots on the other hand impedes the growth of the roots of its own individuals. This probably is the main cause of the poor growth in numbers under conditions which do not favour generative reproduction. However, the longevity of the tussocks and the low mortality of individuals at the early stages of their life determine a high stability of the population at a relatively high level of numbers.

The area occupied by the roots of *F. duriuscula* is much larger that the area occupied by the above-ground parts, hence in the vicinity of the tussocks there always is some bare sand, whereas the cover of the community does not exceed 90%. For the same reason, the growth of young individuals within the clones is only possible when dying senile tussocks release some area, for only then can the root system of the "stifled" juvenile tussocks develop (Rabotnov 1950).

The abundance of a *Cerastium semidecandrum* population depends directly on the number and size of the gaps among the grass tussocks, or pads, and the rosettes of other species of perennial plants present in the community. The main adaptation of *C. semidecandrum* to living in compact communities is its short life history, restricted to the early spring period. Firstly, the life activity is not marked then of the phenologically later perennials, and secondly, in early spring the dune sands are comparatively well supplied with water (Symonides 1974). The production of large numbers of seeds, regardless of the conditions under which the vegetative growth of the plants takes place, makes possible the renewal of the composition of individuals every year. When a comparison is made with other species which reproduce only by seeds, it must be stressed that the mortality of seedlings is relatively low, while their resistance to adverse climatic conditions, especially the ground frost in early spring, is considerable (cf. Symonides 1977).

The stability of a *Jasione montana* population is maintained by other mechanisms. They include above all the very high diaspore production, due to which there is a higher probability to produce a certain number of seedlings, in spite of the low germinating capacity of the seeds. Another mechanism insuring reproduction is the high fruiting fraction and the very low mortality among the individuals which have survived the seedling phase. The plants of *J. montana*, like those of the populations of other species, which are in essence biennial, are able to remain in the juvenile phase for a longer time (even for 3–4 years), if the environmental conditions make it impossible for them to produce seeds in the second growing season (cf. Holt 1972, Werner 1975, Oxley 1977 after Harper 1977). It seems also that a relatively high mortality of seedlings is advantageous for the population, because the development of the plants depends on the attainment by them of the appropriate level of vegetative biomass; a high mortality of seedlings not only eliminates the least fit individuals of a population, but it also creates better conditions of growth for those that survive, and makes it possible for them to attain the generative phases.

A more extensive discussion of the populational phenomena will be included in the last part of the present series (Symonides 1979c).

4. SUMMARY

The study presented in this paper is part of wide-scope studies the aim of which was (1) to follow the changes in the structural and functional characteristics of the populations of 10 selected psammophyte species, taking place during the formation and succession of plant communities, and (2) to analyse the course

and rate of dune overgrowing. The research was carried out in the years 1968–1975, at 10 permanent sites representing different stages of the overgrowing of an inland dune.

In the first and second parts of the series (Symonides 1979a, 1979b) the results are presented of the investigations carried out in initial communities and in loose psammophyte sods. The present, the third, part is devoted to the ecology of the populations of three plant species in communities compact in at least 80%, and to the dynamics of the plants on entirely fixed dune sands. Selected for the study were populations of *Festuca duriuscula*, *Cerastium semidecandrum* and *Jasione montana* found in a community of a variant with *F. duriuscula* (site 9) of the association Festuco-Koelerietum glaucae, and in a community with *F. duriuscula* and only a small admixture of other species (site 10). A detailed description of the methods and of the scope of the research can be found in the first part of the present series (Symonides 1979a).

Changes in the vegetation of both patches were connected primarily with the renewal of the composition of individuals in the populations of perennials; there occurred no significant changes in the qualitative and quantitative structure of the communities studied (Tables I, II). The species which dominated in them throughout the study period was *F. duriuscula* (Figs. 1, 3). At site 9, this species showed an increase in numbers in 1968–1970. A decrease in viability, changes in the age structure, and a slight reduction in numbers in the populations of *Koeleria glauca* and *Festuca psammophila*, with a simultaneous gradual increase in numbers of the characteristic species of the alliance Armerion elongatae, indicated that in the phytocenose slow directional changes were taking place (Fig. 3, Table I). A complete equilibrium of the system was found at site 10 (Table II).

Populations of the species covered by the detailed examinations showed a high stability, in spite of the fact that the dynamic value and the biology of each of them were different. The small variation in numbers of the *F. duriuscula* population over the many years' cycle (except the first three years at site 9) was the result of the longevity of the tussocks and a long prereproductive period, a low reproduction rate, only vegetative (in spite of the production of generative diaspores capable of germinating), and at the same time a low mortality (Figs. 4, 5). Subject to small variations was also the population structure in respect of the percentages of individuals representing different developmental stages, and the flowering and fruiting fractions as well (Fig. 6). Differences in the density of populations 9 and 10 resulted in differences in the formation of the individual-size structure (Fig. 7), and in the rate of development.

The level of numbers in the population of *C. semidecandrum*, an annual, was closely dependent on the number and size of the gaps among the individuals of perennials. Over the yearly cycle the population showed great regular variations in numbers and biomass (Fig. 8); differences in density and frequency in the corresponding periods of different years were insignificant (Fig. 9). The population was characterized by a high degree of aggregation; in the aggregations the effect of density upon the size of the adult individuals was seen in the size structure asymmetry of the population (Fig. 10).

In the population of *J. montana* the reproductiveness, mortality, and in effect the net increase in the particular years varied slightly (Fig. 11). The percentage of germinating *J. montana* seeds was low (1.1%), but owing to their high production, the population was able to maintain a stable abundance. Plants which survived the seedling phase, but did not attain the generative phase in the next growing season, remained juvenile and survived even till the fifth year of life; they usually died after seed production (Figs. 12, 13).

The paper discusses the results of studies concerned with the inner dynamics of relatively durable sod communities on fixed dune sands. An analysis of the population phenomena will be included in the last part of the series (Symonides 1979c).

5. POLISH SUMMARY

Praca jest częścią szerszych studiów, których celem było 1) prześledzenie zmian, jakie zachodzą w strukturalnych i funkcjonalnych właściwościach populacji 10 wybranych gatunków psammofitów w trakcie formowania się i sukcesji zbiorowisk roślinnych oraz 2) zanalizowanie przebiegu i tempa zarastania wydmy. Badania przeprowadzono w latach 1968–1975 na 10 stałych powierzchniach reprezentujących różne fazy zarastania wydmy śródlądowej.

W pierwszej i drugiej części pracy (Symonides 1979a, 1979b) zaprezentowano wyniki badań przeprowadzonych w zbiorowiskach inicjalnych oraz w luźnych murawach psammofilnych. Obecna, trzecia część poświęcona jest ekologii populacji 3 gatunków roślin w zbiorowiskach zwartych co najmniej w 80% oraz dynamice roślinności na całkowicie utrwalonych piaskach wydmowych. Do badań wytypowano populacje *Festuca duriuscula*, *Cerastium semidecandrum* i *Jasione montana* zasiedlające zbiorowisko zespołu *Festuco-*

-Koelerietum glaucae, wariant z *F. duriuscula* (powierzchnia 9) oraz zbiorowisko z *F. duriuscula* i niewielką tylko domieszką innych gatunków (powierzchnia 10). Zakres badań oraz szczegółowy opis metod znajdują się w pierwszej części pracy (Symonides 1979a).

Przemiany roślinności w obu płatach związane były przede wszystkim z odnawianiem się składu osobniczego w populacjach gatunków trwałych; nie zaszły istotne przekształcenia jakościowej i ilościowej struktury badanych zbiorowisk (tab. I, II). W całym okresie badań dominowała w nich *F. duriuscula* (rys. 1, 3), która na powierzchni 9 wykazała w latach 1968–1970 wzrost liczebności populacji. Spadek żywotności, zmiany w strukturze wieku i niewielki spadek liczebności w populacjach *Koeleria glauca* i *Festuca psammophila*, a równocześnie stopniowy wzrost liczebności gatunków charakterystycznych dla związku *Armerion elongatae*, świadczyły o powolnych przemianach kierunkowych zachodzących w fitocenozie (rys. 3, tab. I). Całkowitą równowagę układu stwierdzono na powierzchni 10 (tab. II).

Dużą stabilność wykazały populacje gatunków uwzględnionych w szczegółowych badaniach, pomimo ich różnej wartości dynamicznej i odmiennej biologii. W przypadku populacji *F. duriuscula* nieznacznie tylko zmieniająca się liczebność w cyklu wieloletnim (z wyjątkiem pierwszych 3 lat na powierzchni 9) wynikała z długowieczności kęp i długiego okresu przedrozrodczego, niskiej, wyłącznie wegetatywnej reprodukcji (pomimo produkcji zdolnych do kiełkowania diaspor generatywnych) i równocześnie niskiej śmiertelności (rys. 4, 5). Niewielkim zmianom ulegała także struktura populacji pod względem udziału osobników w różnych fazach rozwoju a także frakcja kwitnienia i owocowania (rys. 6). Różnice w zagęszczeniu populacji 9 i 10 wywołały odmiennie kształtującą się strukturę wielkości osobników (rys. 7) i różne tempo ich rozwoju.

Liczebność populacji jednorocznej efemerycznej rośliny *C. semidecandrum* była ściśle uwarunkowana liczbą i rozmiarem luk między osobnikami gatunków trwałych. W cyklu rocznym populacja wykazywała duże regularne zmiany liczebności i biomasy (rys. 8); w analogicznych okresach różnych lat zagęszczenie i frekwencja zmieniały się nieistotnie (rys. 9). Populację charakteryzowała znaczna skupiskowość; wpływ zagęszczenia w skupiskach na rozmiar dorosłych osobników zaznaczył się w asymetrii struktury wielkości populacji (rys. 10).

W populacji *J. montana* rozrodczość, śmiertelność i – w efekcie – przyrost netto wahały się minimalnie w poszczególnych latach (rys. 11). Nasiona *J. montana* kiełkują w niskim procencie (1.1%), jednak ich duża produkcja zapewnia populacji szansę utrzymania stałej liczebności. Rośliny, które przeżyły fazę siewki i nie osiągnęły faz generatywnych w następnym sezonie wegetacyjnym, przeżywały jako juwenilne nawet do 5 roku życia; przeważnie ginęły po wytworzeniu nasion (rys. 12, 13).

Przedyskutowano wyniki badań odnoszących się do wewnętrznej dynamiki względnie trwałych zbiorowisk murawowych na ustalonych piaskach wydmowych. Analiza zjawisk populacyjnych znajduje się w ostatniej części obecnej serii badań (Symonides 1979c).

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