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THE STRUCTURE AND POPULATION DYNAMICS OF PSAMMOPHYTES ON INLAND DUNES I. POPULATIONS OF INITIAL STAGES

ABSTRACT: The structure and the dynamics are discussed of pioneer populations of *Corynephorus canescens* (L.) P. B. and their role in the fixing of sands, and formation of initial communities. On flying dry sands, they show many features of expansive populations, but their efficiency in fixing sands is fairly low, primarily because of their highly aggregated spatial structure. In more fertile biotopes, free growth of *C. canescens* populations is limited by the competitively stronger grasses: *Festuca psammophila* (Hackel) Krajina and *Koeleria glauca* (Schkuhr) DC. *C. canescens* has been found to have almost completely retreated from areas colonized by *Polytrichum piliferum* Schreb.

KEY WORDS: Inland dunes, psammophytes, *Corynephorus canescens*, populations of initial stages, succession, competition, reproductiveness, mortality, age composition.

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1. INTRODUCTION

Although its floristic and phytosociological aspects have been well described, inland dune vegetation has not so far been the object of wide-scope ecological studies, in spite of the fact that, scientifically, psammophytes no doubt deserve attention. In respect of their adaptation to extreme habitats, a constant deficiency of food and at least a temporary shortage of water, they represent one of the most interesting, ecologically, plant group. Their particular scientific value lies in the fact that they can be used as a model object for both populational and biocenotic investigations. This is due, among other things, to the small number of species and low vegetation density, as a result of which, in dune ecosystems a relatively simple type of relationship is found between the components. Fairly simple, too, is the scheme of the relationship between the subsystems: populations and their environment; an additional value for investigations into these relations being provided by the fact that it is easy to establish the leading factor. Finally, noteworthy is the fact that the ecosystems of poorly fixed inland dunes — ones that are developing, usually at a fast rate — provide an excellent place for studies of the formation, differentiation and succession of plant communities.

It seemed justified to undertake ecological studies of psammophyte populations and communities, the more so as in a not distant future most of the moving, or poorly fixed inland dunes and their specific vegetation will probably become a historic element of the vegetation and landscape of Poland.

The main purpose of the studies here presented was a comprehensive, as much as possible, analysis of phenomena and populational processes, and of the mechanisms controlling all the intrapopulational relations under the conditions of the formation and development of ecological systems at a higher level of organization. Thus the aim was to follow and observe changes in the structure, function and role of the populations of the individual psammophyte species during the process of formation and succession of plant communities. Another objective of the investigations was to study the course and the rate of dune overgrowing by vegetation, and the dynamics of plant communities on sands covering large areas.

The more important results of the studies, continued for several years, will be presented in a series of publications in the order — pioneer species populations and initial plant communities (the present paper), populations and communities characteristic of fixed dunes, with a relatively high density (Symonides — in press a, b, c).

2. STUDY AREA AND OBJECTS

The studies were carried out in the years 1968–1975 in the foreground of a typical dune complex found in the Toruń Basin (Fig. 1). A general description of the geomorphology, soils, climate and vegetation of the study area can be found in the paper by Symonides (1974). The course of the weather conditions during the study period is illustrated by the climographs in Figure 2 (Walter 1962).

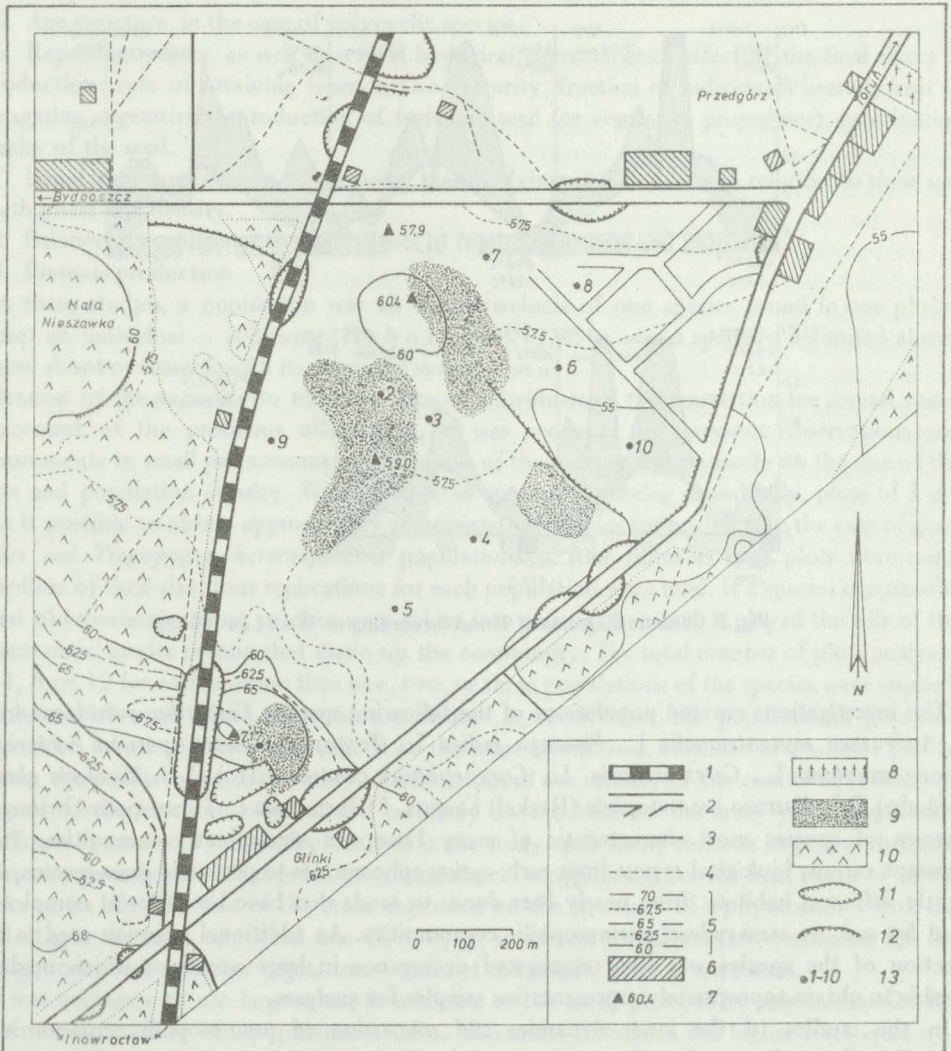


Fig. 1. A sketch map of the study area

1 – railway, 2 – paved roads, 3 – unpaved roads, 4 – paths, 5 – isophyses, 6 – buildings, 7 – elevations (m), 8 – cemetery, 9 – windborne sands, 10 – forests, 11 – clay-pits, 12 – slopes, 13 – study areas

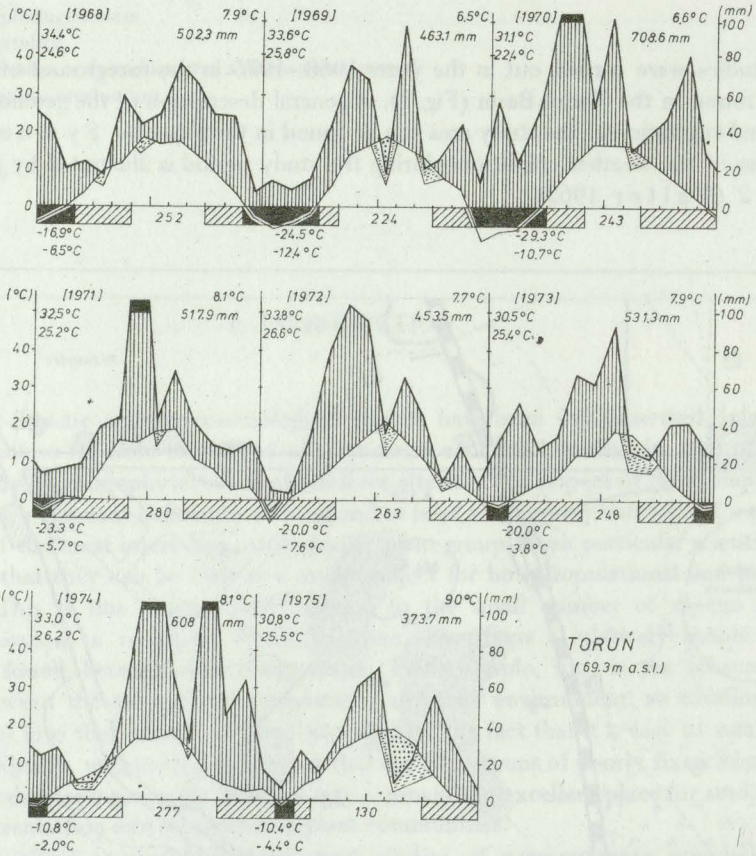


Fig. 2. Climatic diagrams of Toruń (according to Walter 1962)

The investigations covered populations of the following species: *Cerastium semidecandrum* L., *Androsace septentrionalis* L., *Plantago indica* L., *Tragopogon heterospermus* Schweigg., *Jasione montana* L., *Carex arenaria* L., *Corynephorus canescens* (L.) P. B., *Koeleria glauca* (Schkuhr) DC., *Festuca psammophila* (Hackel) Krajina, *F. duriuscula* L. These species belong to a group of species most characteristic of many European sand plant communities. They represent various biological types: from early-spring ephemerides to perennial grass species, and slightly different habitats: from nearly bare dunes to sands that have been almost completely fixed by sod, or semi-ruderal psammophilic communities. An additional criterion used in the selection of the species was their aggregated occurrence in large numbers, which made it possible to obtain appropriately representative samples for analyses.

In the studies of the inner dynamics and succession of psammophilic communities, 10 patches have been taken into account, classified as belonging to the associations: Spergulo-Corynephorum (Tx. 1928) Libb. 1933, Festuco-Koelerietum glaucae Klika 1931 and Corispermum-Plantaginetum indicae Passarge 1957. The main criterion used for the choice of these phytocenoses was the presence of at least one of the species taken into account in the detailed populational investigations.

3. SCOPE OF STUDY AND GENERAL ASSUMPTIONS

The following characters have been taken into account in the analysis of the structural and functional features of the populations:

1. Seasonal and many-years' density dynamics as a measure of population abundance.
2. Frequency in experimental plots during the year, and during a many-years' period, with a basic unit of 0.01 or 0.04 m².
3. Spatial structure in the individual phases of the phenological development of individuals.
4. Structure of the size of individuals, that is, their height or tussock diameter.
5. Age structure, in the case of polycyclic species.
6. Reproductiveness, as well as several biological characteristics affecting the final effect of reproduction: rate of attaining reproductive maturity, fraction of individuals bearing fruit or propagating vegetatively, production of fruit and seed (or vegetative propagules), germination capacity of the seed.
7. Population mortality in the growing season, dying of individuals in relation to their age, growth phase and density.
8. Balance of numbers as the final effect of reproductiveness and mortality.
9. Biomass production.

In these studies, a population was all the individuals of one species found in one phytocenose; an individual — following R a b o t n o v (1950) — was a spatially delimited above-ground shoot or tussock with its own root system.

Because of the necessity to trace the fate of individuals of the population for several years, on account of the problems undertaken, it was necessary to carry-out observations and measurements in small permanent plots. The size of these depended primarily on the size of the plants and population density. With small-sized species, occurring abundantly, plots of 1 m² made it possible to obtain appropriately representative samples for analyses; in the case of grass species and *Tragopogon heterospermus* populations — four times as large plots were used. Regardless of their size, four replications for each population were used. If a species occurred in several phytocenoses, those patches were taken into account in which it played the role of the characteristic species or one that made up the community. The total number of plots analysed was 4, 8 or 12 for each species; thus one, two, or three populations of the species were studied.

The use of small plots might arouse doubts as to whether the populational processes observed on a "micro" scale are realized to the same extent in a biochore as a whole, that is, whether the results agree with reality. Verifications of the validity of the results in relation to the scale of the biochore were carried out only on the basis of the many-years' population abundance dynamics in the small plots, and in the study areas many times as large, per the same unit space, assuming that changes in the abundance of a population are the final result of all the aspects of its life. The size of the areas depended on the structure of a phytocenose: with the initial stages the area size used was 16 × 16 m, to obtain a representative material for the investigations; with a thicker vegetation — areas of the size 10 × 10 m were used.

It was necessary to use large areas, in addition to the small plots, to be able to describe the spatial macrostructure of a population, and to determine its role in the higher level system — phytocenose. At the same time, they were used as an object for studying the structure and dynamics of plant communities. The scope of the studies included an analysis of the specific composition, frequency, abundance, degree of cover, and the biomass of all the components of a phytocenose. Several years later it was possible on their basis to assess the course and the rate of dune overgrowing by vegetation

To obtain a correct assessment of the competitive phenomena between individuals of the same population, and between populations of different species, several simple experiments have been carried out under natural conditions. They consisted in the removal or introduction into the study areas of certain species, or a specified number of their individuals.

Some of the results have been interpreted with climatic and soil data taken into account.

4. METHODS

4.1. STUDY PERIOD, FREQUENCY OF MEASUREMENTS, ANALYSES AND OBSERVATIONS

Field studies were carried out from March 1968 to July 1975. In the measurements and observations carried out in the plots, the whole growing season was always taken into account. Their frequency was adjusted to the length of the developmental cycle and the developmental stage of the species. During the first five years, annuals were examined at 3–5 days' intervals. The same frequency was used during the germinating and fixing of the seedlings in the case of biennial and perennial species. For the remaining developmental phases of these species the time intervals between successive measurements were 2–3 weeks. From 1973 on, a lower frequency of measurements and observations was used – 10 days in spring, and 20–23 days in the remaining seasons.

In the study areas, measurements and analyses were carried out 2–3 times a year, during the full growth of the main components of the phytocenose.

The experimental studies were carried out in the years 1972–1975. Apart from this, the growing season of 1973 was devoted to collecting material to be used in the assessment of the level of biomass and production of the population.

4.2. FIELD OBSERVATIONS AND MEASUREMENTS

In the first study year, 10 square areas were set up in the centre of the phytocenoses selected. Each was subdivided into plots of 1 m^2 (the size of the area being 100 m^2), or 4 m^2 (the size of the area being 256 m^2). In accordance with the adopted assumptions, the study areas differed by the degree of sand fixing, floristic composition, number of species present and, to a lesser extent, habitat properties. Their vegetation represented different associations, or different facies or phases of development of the association. In each area the dominating, in respect of numbers or biomass, component of the phytocenose was the population of one of the species listed in Section 2.

In each area four plots were selected for detailed populational studies of a particular species. Two main criteria were taken into account: firstly, the plots were to reflect, as fully as possible, the specific composition and the quantitative relations between the components of the phytocenose, that is, they were to constitute an area representative of it; secondly – within each study area plots were to be selected so that they would be as similar as possible in respect of the composition and number of individuals of the particular species. Each plot was divided into 100 square basic units (the "microplots").

On each measurement day the following were recorded for the plots:

1. Number of individuals, counted directly, or — in the case of the seedlings of *Corynephorus canescens* and *Cerastium semidecandrum* — by the estimative method (Symonides 1977).

2. Position of the individuals within the plots, by specifying the coordinates, or marking on sketch maps; except for the seedlings and individuals of annual species, each individual was assigned a registration number.

3. Size of individuals, i.e., their height, or the diameter of tussocks across the broadest portion, with an accuracy to the nearest 0.2–0.5 cm.

4. Age of individuals, expressed in absolute units of time or as a developmental phase: seedling, juvenile, mature, old.

5. Phenological phases of individuals. Several phenophases were distinguished: seedling, vegetative growth, budding, flowering, fruiting, dissemination, dormance.

At the beginning of the growing season, and during the flowering or fruiting of the main components of a community the following data were recorded: specific composition, frequency, cover, and the number of individuals of each population in all the plots of a study area.

4.3. BIOMASS PRODUCTION EVALUATION

The yearly organic matter production by the populations under study was estimated by Traczyk's (1967) method, with some modifications applied in the evaluation of the individual production. The estimation was made several times during the growing season; each of the samples to be analysed consisted of a specified number of plants of the same age, developmental phase and size of the individuals. Owing to this, it was possible to: (1) take into account in the total production of the population the biomass of the individuals dying at the different growth stages, (2) estimate the contribution to the production of individuals of different age, (3) assess the annual production of a population in permanent plots (without removing the plants) on the basis of the number, age, size and developmental phase of the individuals that died and those that survived in a population in a particular year.

Plants to be used for the analyses were dug out in their entirety in the vicinity of the study areas. After cleaning and sorting the underground and the above-ground parts separately, the samples were dried for 48 hours at 85°C and weighed to the nearest 0.01–0.001 g. The frequency of the analyses, the size and the number of the samples, and the method of calculating the individual production depended on the length of the developmental cycle of a species, and on the size of the plant.

Samples of annual species were collected in the seedling, vegetative growth, budding, flowering and fruiting phases. Apart from the seedlings, 3–5 size classes of individuals were taken into account. Each sample consisted of 50–100 plants. The average individual weight in each sample corresponded to the average individual production in a given growth phase and size class.

In the case of biennial species, individuals in the first and in the second year of life were analysed simultaneously. Samples were collected 5 times in a growing season, from the time of appearance of the seedlings, or of the above-ground parts of the second-year individuals. On each date 50 individuals in 5 size classes were taken; the seedlings were considered jointly. The production of the first-year individuals was calculated in a way similar to that used for the annuals; likewise — the above-ground parts of the second-year individuals. The root production

in the second year was the difference between the current weight and the minimum weight as determined at the beginning of the growing season.

In the populations of perennials, production was analysed separately for the seedlings, one-year old individuals, two-years old individuals, several-years old individuals flowering or fruiting, and old individuals, or ones with clear signs of ageing. The mean seedling weight was calculated from the weight of 50 individuals of this phase. Samples of the remaining individuals were collected 6 times during the growing season, 20 individuals each time, individuals grown from seed and those by vegetative propagation being analysed separately. For mature and old individuals 3–5 size classes were used. The average individual production of each age group and size class was determined by subtracting the initial weight, as estimated at the beginning of the growing season, from the current weight at the time of measurement.

The estimates of the production of individuals differing by their age and size provided the basis for the estimation of the productivity of populations in permanent plots during the successive years. For each plot the number of individuals and their varying size, age and developmental stages were recorded; it was, therefore, possible to assume for each individual in the plots the most likely value of biomass production, and to add to the total production of a population the biomass of the individuals that died. The production of a population in a plot was the sum total of the production of a given number of individuals of different age and size.

In the study area the level of biomass of all populations was determined at the time of full fruiting of the dominant species. As in the plots, the size of the individuals was converted to their weight determined once in 1973 on the basis of an analysis of the weight of individuals collected at random outside the study area. For the dominant species 5–6 size classes were taken into account, 50–100 individuals of each class; in the case of species occurring in small numbers, 10–20 individuals were collected.

4.4. DIASPORE PRODUCTION EVALUATION

At the time of fruiting, in each plot the fruiting individuals of the populations were counted, and in the case of grasses – the number of fruiting shoots of a tussock were also counted. Outside the study area the fruits were counted in a hundred randomly selected individuals, and then the seeds of a hundred, also randomly selected fruits. From the average number of seeds in a fruit, and the average number of fruits per an individual it was possible to estimate the production of diaspores by an average individual of a population. The product obtained by multiplying this production by the number of fruiting individuals was the production of diaspores in a plot.

In the case of grasses a slightly different procedure was used. In the assessment of the individual production of diaspores taken into account were tussocks of similar diameters and of the same number of panicles or spikes as in the plots, 10 for each variant. The average number per a tussock of a given size and number of fruiting shoots was attributed to an analogous tussock in the plot. Their sum total was the production of diaspores in a plot.

4.5. STATISTICAL ANALYSIS OF RESULTS

The elaboration of the results for the populations of the individual species consisted in using the following procedures: (1) a statistical description of the characters studied, that is, calculating the mean (\bar{x}), variance (S^2) and the standard deviation (s), (2) assessment of the

homogeneity of a sample and its representativeness for the scale of a biochore, a sample always consisting of 4 plots, (3) verification of the hypothesis concerning the variation of some of the characters during the growing season, and the successive years. Statistical conclusions were always drawn at a 5 per cent error risk.

The homogeneity of a sample was tested by the method of variance analysis with a double classification (O k t a b a 1966), the objects being the 4 replications, and the blocks — the years. The representativeness of a sample for the scale of a biochore was assessed for the density per unit surface by verifying the null hypothesis of a lack of differences between the average density in the plots, and the average density in the study area, by the Cochran-Cox test (O k t a b a 1966).

Differences in the values analysed between the individual years were verified by the variance analysis test in double classification, the objects in this case being the years. If a character studied was expressed as a fraction, then for the subsequent statistical analysis the empirical data were transformed by means of the function: $\varphi = 2 \arcsin \sqrt{p}$, where p is the fraction value (Zieliński 1972).

The χ^2 test for the homogeneity of a statistical population was used to verify the significance of differences: (1) between the fractions of the quadrats (in the study area and plots) with the occurrence of at least one individual of a population in the individual years, (2) between the fractions of the individuals that died in the particular years, (3) between biomass production by individuals of different age in different years.

In addition, if necessary, for the characters studied the following statistical techniques were used:

1. To determine the spatial micro- and macrostructure of a population, the type of spatial distribution of individuals in the plots and study area was tested by comparing the value of the arithmetic mean and of the variance (V a s i l e v i č 1969) for the number of individuals on a surface area of 0.01–0.04 m² and 1–4 m². If the two values were similar, an additional verification of the hypothesis on the accordance of the distribution of individuals with Poisson's distribution was carried out by the χ^2 test for consistency (O k t a b a 1966).

2. To establish the effect of density on the size of individuals, correlation coefficients were calculated between size classes of the individuals and their number on the basic unit surface areas (0.01 or 0.04 m²). Correlation coefficients were also calculated for the evaluation of the relationship between the density and biomass production in the plots.

3. A comparison of the average size of an individual of a population and the average value of the individual production of diaspores in different years was carried out by using the single analysis of variance test (G r e ě 1974).

5. RESULTS

5.1. SAND COLONIZATION AND THE DEVELOPMENT OF INITIAL COMMUNITIES

The initial stage of sand fixing and settling of the pioneer plants was investigated at two almost "bare" sites each of 256 m². Site 1 was located on a southern slope of an elevation with an inclination of 5°. This was a large area of sands blown away by wind, with no soil cover. On the dry, easily heated bare sands there the conditions for plant growth were extremely

unfavourable. In the first study year only 117, mostly young, tussocks of *Corynephorus canescens* were found and 1760 small specimens of *Spergula vernalis* Willd., covering only 3.2 m² of the area. The two species formed 16 aggregations, clearly separated by a space of moving sand, fixing jointly about 7% of the study area.

C. canescens, as could be judged from the age of the tussocks, had settled there probably 3–4 years prior to the beginning of the studies. The first individuals of *S. vernalis*, which settle on moving sands only near the grass tussocks, arrived there also (probably) only after *C. canescens*.

In the 8-year observation period the development of the initial vegetation proceeded exclusively towards an increased number of individuals of both components of the community (Fig. 3): there occurred a 40-fold increase in the abundance of *C. canescens* population, and over 4-fold of *S. vernalis*. The number of species did not increase, although in 1972 there

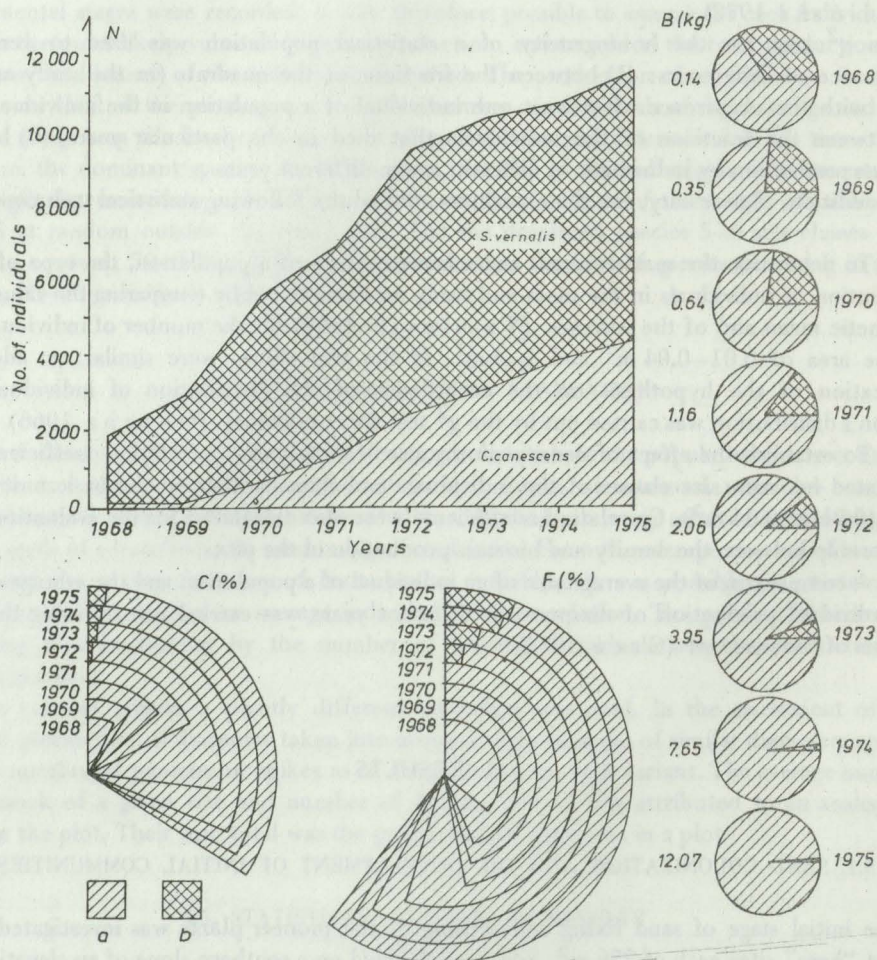


Fig. 3. Variations of numbers and quantitative relations between community components (N), total biomass and percentage of the individual components (B), cover (C) and plant frequency (F) on site 1
a - *Corynephorus canescens*, b - *Spergula vernalis*

already appeared a small number of seedlings belonging to *Festuca psammophila*, *Koeleria glauca*, *Pinus sylvestris* L., and *Tragopogon heterospermus*; they always died within 2–3 months.

The numerical predominance of *S. vernalis* persisted until the end of the investigations, in spite of the much faster growth of the populations of *C. canescens*. Seedlings of both species usually emerged near the parent individuals, due to which the density of the aggregations increased, and so did the areas occupied by them; only five new aggregations formed.

During the eight years the populations of the two species fixed about 70 m² of bare sands. However, 2/3 of the surface area remained bare until the end of the investigations, and in spite of an almost 6-fold growth in the total number of individuals, the growth in frequency was only 23% (Fig. 3).

There was a very clear, over 86-fold, increase in the plant biomass of the community during the study period; also the contribution of *C. canescens* grew from year to year. The contribution of *S. vernalis* to the total biomass decreased from 36.7% in 1968 to as little as 1% in the last year of study (Fig. 3).

Site 2 was located within a large stretch of sands in a small land depression. The sands found there were as infertile as at site 1, but were moister and did not get so hot during the summer heat-waves (cf. Symonides 1974). As at site 1, the vegetation consisted exclusively of two species: *C. canescens* (142 individuals), and *S. vernalis* (3040 individuals). Similarly to site 1 also, an aggregated spatial structure of the populations of both species was found, and a low frequency and low degree of cover (Fig. 4). In accordance with the objectives of the investigations, the analysis of the specific composition and vegetation structure on both sites during the eight years was to answer the question: if and to what extent small differences in habitat conditions can affect the colonization by plants, and thereby the course of the overgrowing of a dune with plants.

The results were rather striking. First of all, the floristic list of site 2 had increased considerably. *Polytrichum piliferum* appeared already in the second year. In the following years further species settled there in the following order: *Festuca psammophila*, *Koeleria glauca*, *Helichrysum arenarium* (L.) Moench, *Pinus sylvestris*, *Sedum sexangulare* L., *Thymus serpyllum* L., *Veronica dillenii* Cr., *Gypsophila fastigiata* L., *Plantago indica*, *Androsace septentrionalis*, *Cerastium semidecandrum*, *Viola canina* Rchb., *Pulsatilla pratensis* (L.) Mill., *Calluna vulgaris* (L.) Salisb. In 1975, the total number of individuals of the new-arrived species of flowering plants increased up to 192, which represented 14.7% of all flowering plants in the observation area. Particularly numerous were the grasses: *F. psammophila* and *K. glauca* (46.8% of new individuals).

A rapid spread was recorded for *Polytrichum piliferum*. The originally loose synusiae of this moss, always appearing near *C. canescens* tussocks, formed thick sods within 2–3 years, and filled a large proportion of the spaces between the grass tussocks. In 1973, *P. piliferum* covered 50%, and in 1975 – as much as 71% of the total area (Fig. 4).

Different from site 1 was also the fate of the two primary components of the community. A growth in number of *C. canescens* and *S. vernalis* occurred only up to 1972; in the following years fewer and fewer seedlings of both species were found, and at the same time a mass withering of *C. canescens* tussocks was recorded. Only those new individuals of *C. canescens* survived which had grown in places not occupied by *P. piliferum*. The frequency of *C. canescens* grew gradually to attain 89% (Fig. 4) at the end of the investigations.

In the years 1968–1975, the total biomass of the flowering plants on site 2 increased nearly six times, although the number of individuals in this period decreased by more than a half

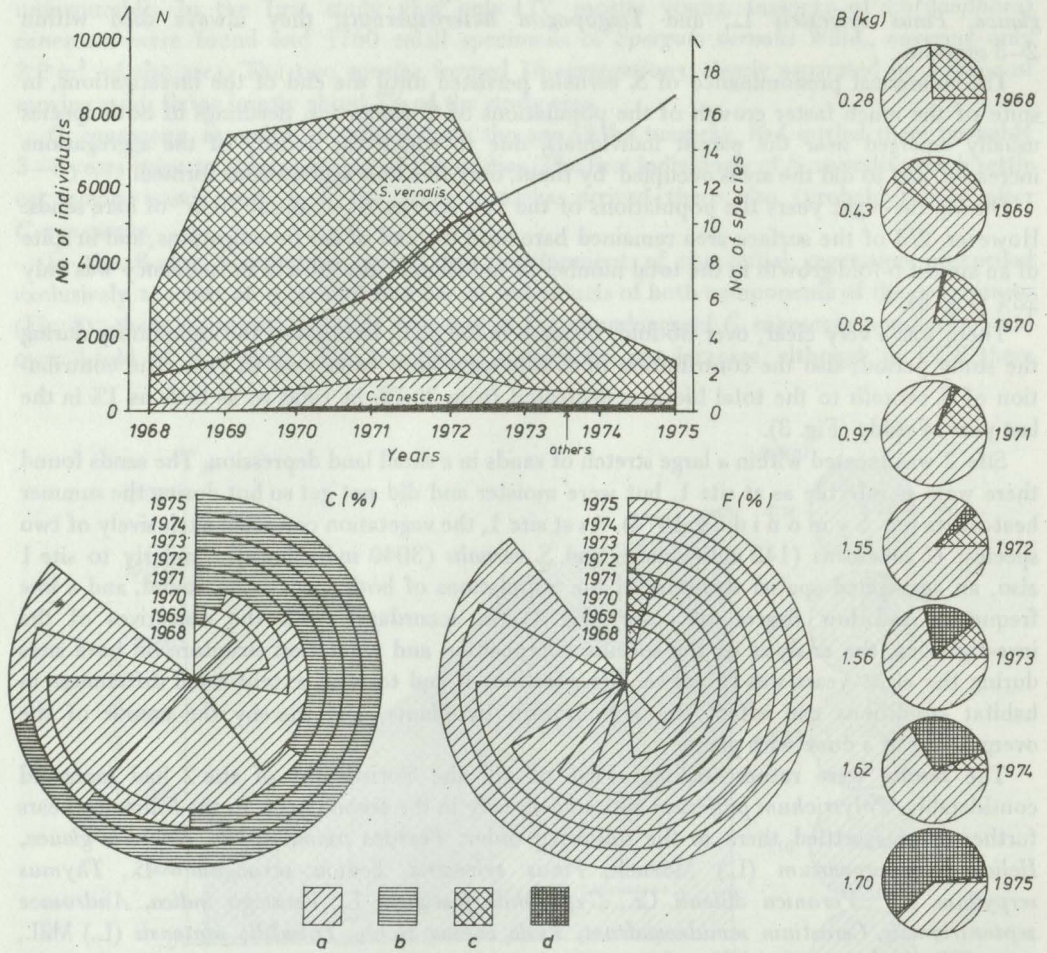


Fig. 4. Variation of the number of species (thick line) and of individuals (thin upper line) and quantitative relations between the components of community (N), total biomass and percentage of individual components (B), cover (C) and plant frequency (F) on site 2
a – *Corynephorus canescens*, b – *Polytrichum piliferum*, c – *Spergula vernalis*, d – other species jointly

(Fig. 4). The fastest biomass increase rate was recorded for the years 1968–1972, that is, at the time of the fast growth in number of *C. canescens*. In 1972, the level of biomass was only 9% lower than the maximum level. The percentage of “new” species increased from year to year, up to 60.3%, in the last year, of the total biomass.

Studies on the dynamics of the initial communities were carried out at site 3, representing a poor patch of *Spergulo-Corynephorum* on sands that were to a large extent fixed and with a thin layer of raw humus. In 1968, 35% of the surface was covered (90 m²), the frequency of plants being 90.6%.

The community consisted of 12 species; numerically dominating were – *S. vernalis* (1315), *C. canescens* (1204), *F. psammophila* (878) and *K. glauca* (548). Individuals of the remaining species jointly represented 18.7% of the total number of plants (Fig. 5). They belonged to the

following species: *Veronica dillenii* (385), *Rumex acetosella* L. (256), *Scleranthus perennis* L. (112), *Hieracium pilosella* L. (54), *Helichrysum arenarium* (34), *Thymus serpyllum* (4). Of the cryptogamous plants *Polytrichum piliferum* covered about 3 m², and *Cornicularia aculeata* (Schreb.) Ach. – about 2.5 m².

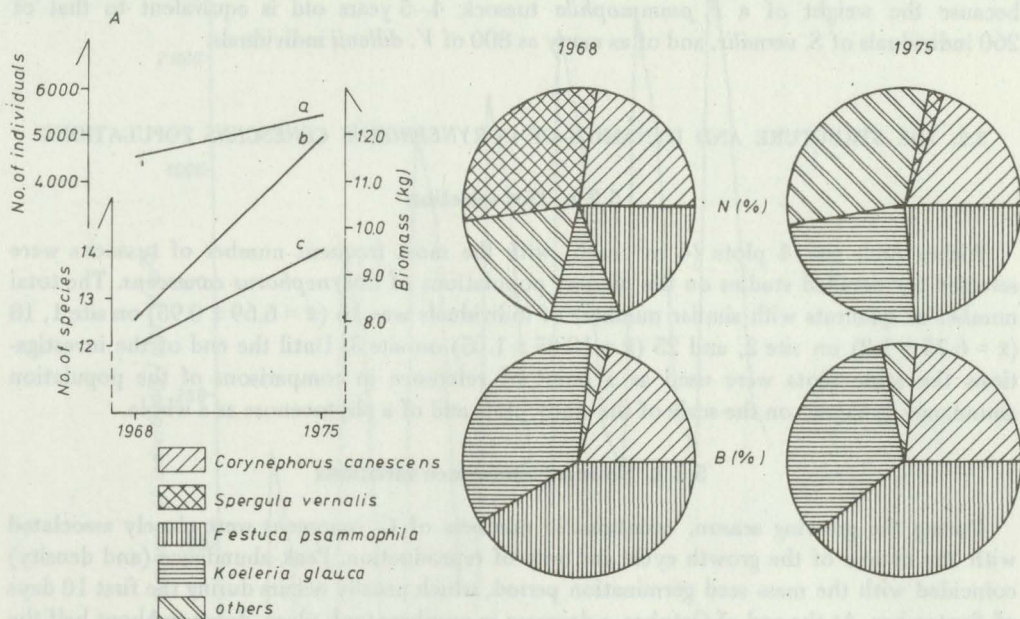


Fig. 5. Comparison of the number of individuals (a), biomass (b), number of species (c) (A) and of the quantitative relations (N) and the percentage in the biomass (B) of individual components of the community in 1968 and 1975 on site 3

The dominant species most often occurred jointly in several loose aggregations scattered throughout the area. The remaining species formed a mosaic, characteristic of the dune vegetation, made up of one-, or rarely two-species patches, individuals of sporadic species being found in only 1–2 quadrats.

During the eight years, the floristic list of the community was increased by a further 3 species: *P. indica* (from 1973), and *A. septentrionalis* and *T. heterospermus* (both from 1974). *V. dillenii* retrated in 1972.

The number of individuals increased by only 17% relative to 1968, but the numeric ratios between the populations of dominants changed (Fig. 5). A steady decrease in the number of individuals was seen in *S. vernalis* (from 1315 to 27), and an increase in *F. psammophila* (by 356 individuals) and *K. glauca* (by 83 individuals). Noteworthy is the fact that although during the first three years of study numerous seedlings of both species appeared and the grasses reproduced only generatively, in following years seedlings emerged in small numbers, and they died in a short time thereafter, whereas 95% of the new individuals originated from vegetative reproduction. In the successive years, the level of numbers of *C. canescens* varied slightly; in 1975 the number of tussocks counted was only one less than in 1968.

In spite of the relatively small increase in the number of individuals, the surface cover increased by 21.9% (56 m²), and the biomass of the community by as much as 48% (Fig. 5).

Throughout the study period, 90% of the biomass was the biomass of the grasses. Thus the increase in the level of the biomass of the community was connected primarily with an increased abundance of the grass populations and the increasing proportion of older tussocks. The proportion of small therophytes (*S. vernalis*, *V. dillenii*) constituted only a fraction per cent of the total biomass, in spite of the large number of individuals. This is understandable, because the weight of a *F. psammophila* tussock 4–5 years old is equivalent to that of 260 individuals of *S. vernalis*, and of as many as 800 of *V. dillenii* individuals.

5.2. THE STRUCTURE AND DYNAMICS OF *CORYNEPHORUS CENESCENS* POPULATIONS

5.2.1. Plot selection

Within each site 4 plots (4 m² each) with the most frequent number of tussocks were selected for detailed studies on the pioneer populations of *Corynephorus canescens*. The total number of quadrats with similar numbers of individuals was 16 ($\bar{x} = 6.69 \pm 0.95$) on site 1, 18 ($\bar{x} = 6.75 \pm 1.2$) on site 2, and 25 ($\bar{x} = 13.25 \pm 1.05$) on site 3. Until the end of the investigations the same plots were used as a point of reference in comparisons of the population abundance dynamics on the scale of the study plots and of a phytocenose as a whole.

5.2.2. Seasonal abundance variations

During the growing season, variations in numbers of *C. canescens* were closely associated with the course of the growth cycle and way of reproduction. Peak abundance (and density) coincided with the mass seed germination period, which usually occurs during the first 10 days of September. At the end of October, a decrease in numbers took place, down to about half the maximum level, whereafter the rate of decrease in numbers was slower. A relatively stable level of numbers, a low one relative to the maximum level, was attained by the population only in the flowering period (June). In the fruiting phase it was usually only the single tussocks that usually withered, and during a dry and hot summer the mass withering of tussocks continued until the first early-autumn rains, after which the first seedlings emerged.

The main course of the seasonal variations in number of the populations¹ compared was similar (Figs. 6, 7). The differences related to the variation amplitudes, that is, the absolute number of individuals by which the population abundance increased or decreased.

In population 1 a particularly great amplitude of seasonal variations in the density was found (Fig. 6). During the period of mass germination each year, the number of individuals was 20–30 times as large as during the fruiting period, and in 1969, in spite of the drought that had preceded the germination (cf. Fig. 2), the abundance of this population increased as much as 47 times, relative to the minimum level.

In population 2, only in the first study year a considerable, 35-fold, increase in the number of individuals was found during the growing season. In the subsequent years the amplitude of variations in number gradually decreased, so much so that during the germination period in 1974 there were only 1.09 times as many individuals as during the fruiting (Fig. 7).

The maximum number of individuals in population 3 was each year 6.1–7.2 times as high as the minimum number (Fig. 7).

¹ The populations have been given the same numbers as the areas from which they came from.

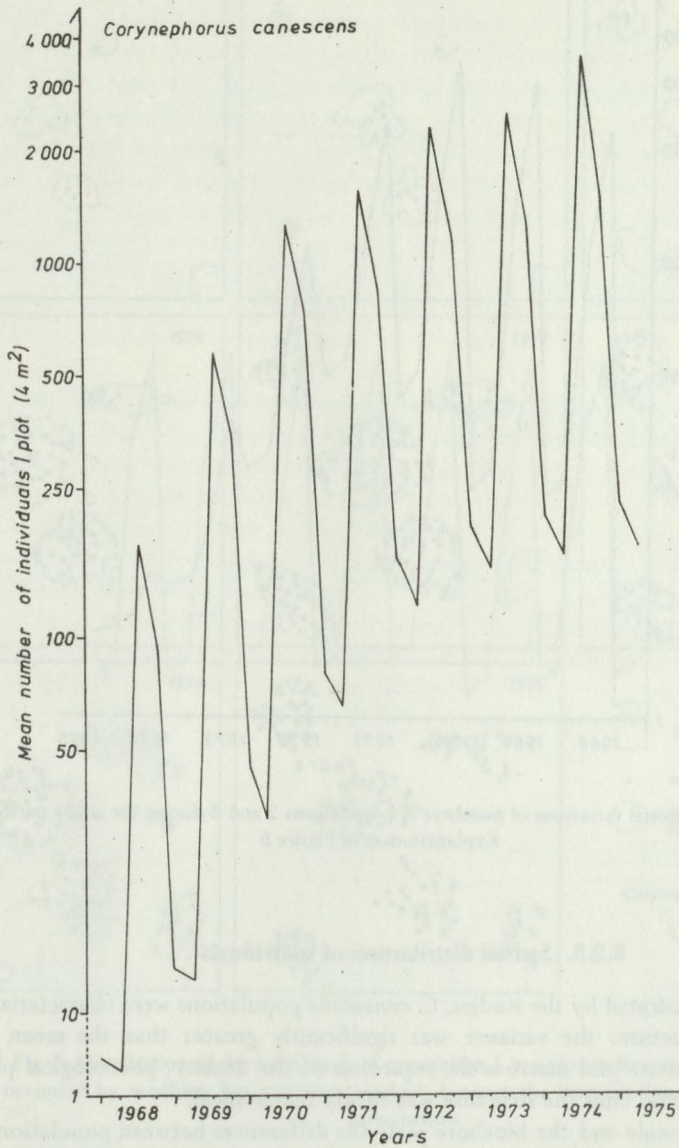


Fig. 6. Seasonal variations of numbers in population 1 during the study period. Points in each year represent population density at the beginning of the growing season (March), at full flowering (June), in the period of maximum germination (September) and at the end of the growing season (end of October or beginning of November)

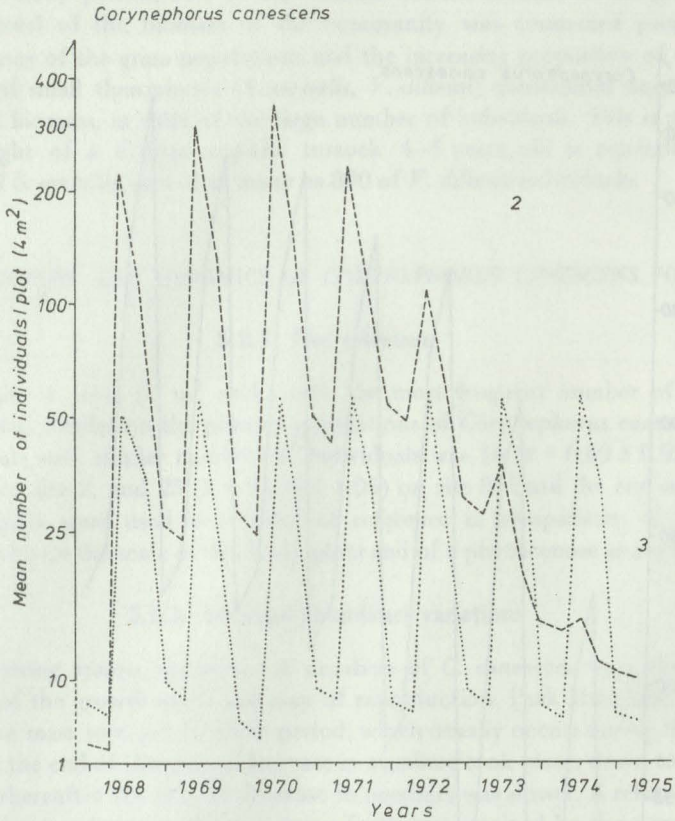


Fig. 7. Seasonal variations of numbers of populations 2 and 3 during the study period
 Explanations as in Figure 6

5.2.3. Spatial distribution of individuals

As has been demonstrated by the studies, *C. canescens* populations were characterized by an aggregated spatial structure: the variance was significantly greater than the mean value of density on both the micro- and macro-scale, regardless of the density, phenological phase and environmental conditions. Thus the structure was clearly hierarchical.

On both the micro-scale and the biochore scale the differences between populations related primarily to the number of aggregations and their density, i.e., number of individuals making up an aggregation. It was only the "size" of the aggregations, that is, the number of individuals present in them, that clearly changed in the population from year to year, and to a lesser extent the area occupied by the individual aggregations. The number of aggregations within the plots and sites remained almost the same, regardless of the type of abundance dynamics. Figure 8 presents a charted distribution, as an example, of population 1 individuals in one of the plots in 1968–1975. It can be concluded from it that during the eight years only two new aggregations formed, only one of which survived until the end of the studies, although there had been an

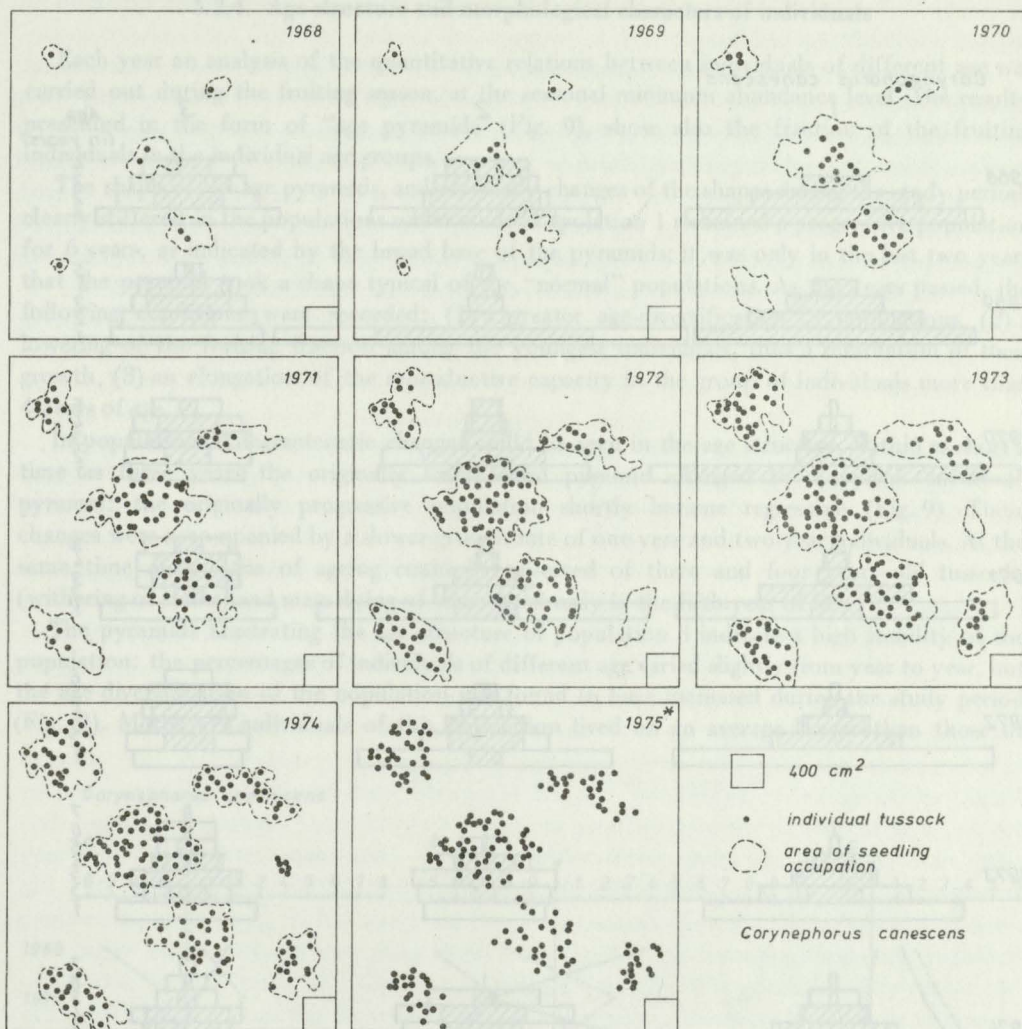


Fig. 8. Distribution of the individuals of population 1 in a plot in the years 1968–1975

*The area occupied by seedlings has not been marked, because the investigations were completed before germination

almost 25-fold increase in the number of individuals. From Figure 8 also it can be concluded that even in the period of the seasonal peak abundance the spatial structure type did not change, relative to the minimum level of numbers, because seedlings emerge in the closest vicinity of the parent individuals.

A similar situation was seen in both the other populations; in population 3 plots not only was a fixed number of aggregations maintained throughout the study years, but also a very similar abundance of the aggregations in the same months of different years.

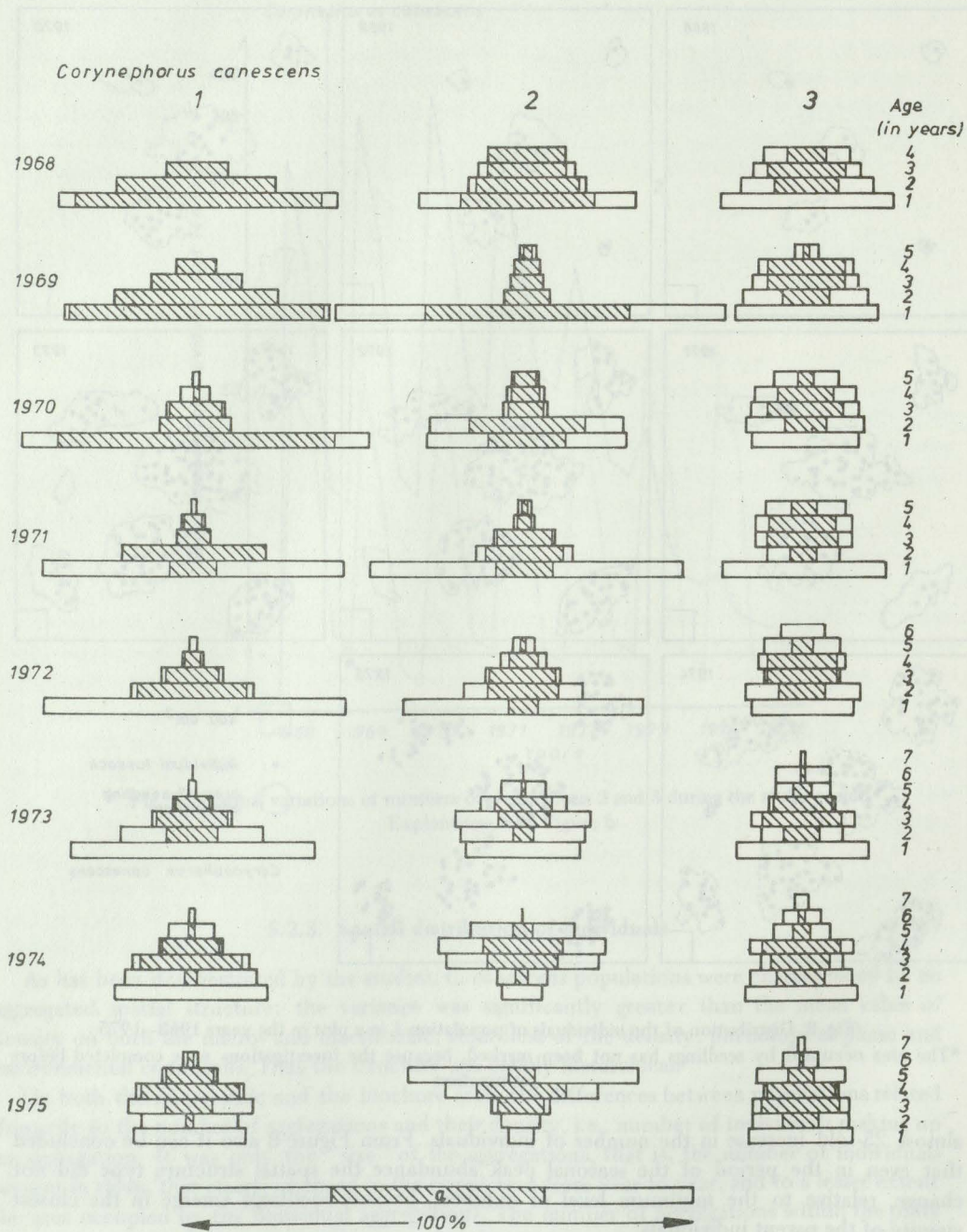


Fig. 9. Age structure of populations 1, 2, 3 during the study period (in per cent)
 a — fraction of fruiting individuals. Average life span of an individual of population 1 — 7.76 ± 0.56 ,
 population 2 — 7.81 ± 0.37 , population 3 — 8.65 ± 0.20 (in months)

5.2.4. Age structure and morphological characters of individuals

Each year an analysis of the quantitative relations between individuals of different age was carried out during the fruiting season, at the seasonal minimum abundance level. The results, presented in the form of "age pyramids" (Fig. 9), show also the fraction of the fruiting individuals in the individual age groups.

The shape of the age pyramids, and especially changes of the shapes during the study period, clearly differed in the populations under study. Population 1 remained a progressive population for 6 years, as indicated by the broad base of the pyramids; it was only in the last two years that the pyramid took a shape typical of the "normal" populations. As the years passed, the following conditions were recorded: (1) a greater age-diversification of populations, (2) a lowering of the fruiting fraction among the youngest individuals, thus a retardation of their growth, (3) an elongation of the reproductive capacity in the group of individuals more than 4 years of age.

In population 2, characteristic changes could be seen in the age structure. Within as short a time as three years the originally broad-based pyramid changed to a typical "inverted" pyramid: the originally progressive population shortly became regressive (Fig. 9). These changes were accompanied by a slower growth rate of one-year and two-year individuals. At the same time clear signs of ageing could be observed of three and four years old tussocks (withering of stalks) and mass dying of tussocks already in the fifth year of life.

The pyramids illustrating the age structure of population 3 indicate a high stability of the population: the percentages of individuals of different age varied slightly from year to year, but the age diversification of the population was found to have increased during the study period (Fig. 9). Moreover, individuals of this population lived on an average longer than those of

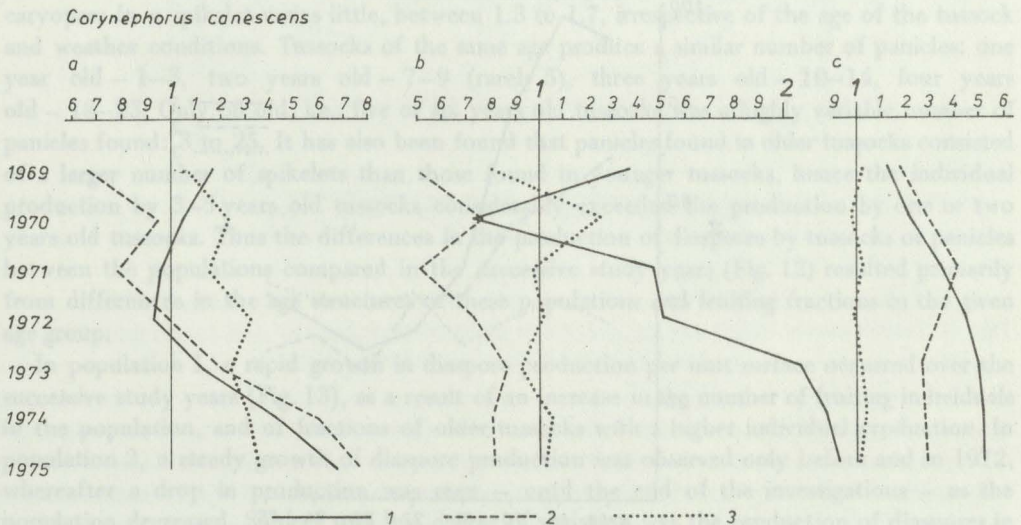


Fig. 10. Tussock diameter (a), number of panicles (b) and the number of spikelets in one panicle (c) of an average individual of populations 1, 2, 3 in the years 1968–1975

The comparative unit (vertical lines) is the values of the characters in 1968: population 1: a – 5.38 cm, b – 5.85, c – 39.2, population 2: a – 7.13 cm, b – 10.80, c – 38.4, population 3: a – 9.76 cm, b – 11.25, c – 40.50

populations 1 and 2, and they usually attained generative maturity at a later time, only, in the second and third year of life.

In the analysis of the morphological characters the following were taken into account: tussock diameter, number of panicles and the number of spikelets in a panicle. The analysis has shown that in a group of individuals of the same age these characters varied very little from year to year. They differed insignificantly also between individuals of the same age but of different populations. Thus the variations in the values of characters in an average individual of each population in the study years (Fig. 10) resulted primarily from changes in the age structure of a population. Because tussocks of the same age are of similar size, regardless of the habitat and study year, the size structure of a population corresponds to its age structure.

5.2.5. Reproductiveness

The following were taken into account in the estimation of the reproductiveness: (1) fraction of fruiting individuals of the population, (2) diaspore production, (3) number of seedlings, (4) contribution to reproduction by individuals of different age.

As a result of a fast growth rate of the young individuals, which flowered and produced caryopses the following year, the fruiting fraction of population 1 amounted at the beginning to over 90% (Fig. 11).

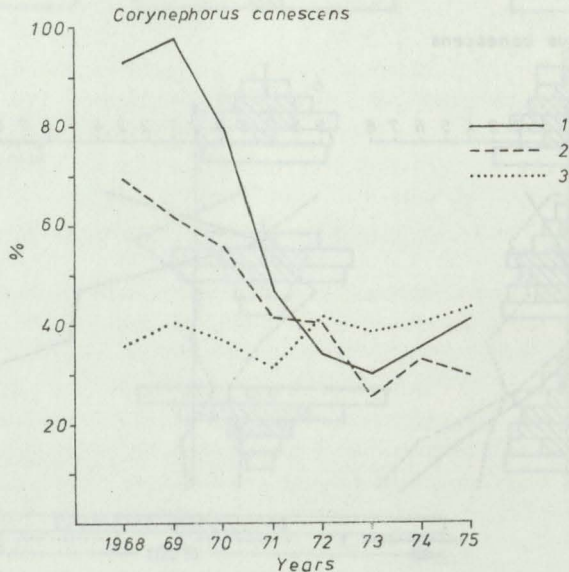


Fig. 11. The fruiting fraction of populations 1, 2, 3 in consecutive study years (100% – total number of individuals in population)

The fast decrease, from year to year, of the percentage of the fruiting individuals of the population resulted from the delayed development of the one- and two-year individuals which predominated numerically. In the last year, four years old individuals represented as much as 22% among the individuals which fruited for the first time. At the same time, the upper age limit of reproductive capacity was shifted: in 1973 none of the five years old plants flowered, while two years later nearly all the five and six years old individuals flowered and fruited (cf. Fig. 9). Hence, during the last two years a new increase was seen in the fruiting fraction of the population (Fig. 11).

Similar changes occurred during the study period in population 2. The considerable decrease in the fruiting fraction — to 24% in 1973 — had been caused not only by the delayed, as compared with the first years, maturing of the young individuals, but also by the premature loss of the reproductive capacity of the four and five years old individuals. In the last study year, only 11% of all the five years old tussocks produced caryopses, and none of the tussocks in the second year of life produced fruit.

A comparatively small (36–43%) fruiting fraction, that changed little during the study period, was found in population 3 (Fig. 11). During the eight years, more than half of the individuals fruited only in the third year of life, and never earlier than in the second year. The particular individuals produced fruits for 4–5 years. Although they flowered, individuals above six years of age never produced caryopses.

On account of the diverse abundance and age structure of the populations, and their variations from year to year, the production of caryopses has been presented relative to the size of the plot, and per one fruiting tussock and one fruiting shoot.

The value of the production of caryopses by a population is on the one hand the function of the number of fruiting tussocks, and on the other hand — of the number of collective fruits in a tussock and the number of spikelets in a collective fruit. As a character, the number of caryopses in a spikelet varies little, between 1.3 to 1.7, irrespective of the age of the tussock and weather conditions. Tussocks of the same age produce a similar number of panicles: one year old — 1–3, two years old — 7–9 (rarely 5), three years old — 10–14, four years old — 18–23. Only on old, i.e., five or six years old tussocks was a highly variable number of panicles found: 3 to 25. It has also been found that panicles found in older tussocks consisted of a larger number of spikelets than those found in younger tussocks, hence the individual production by 3–5 years old tussocks considerably exceeded the production by one or two years old tussocks. Thus the differences in the production of diaspores by tussocks or panicles between the populations compared in the successive study years (Fig. 12) resulted primarily from differences in the age structures of these populations and fruiting fractions in the given age group.

In population 1, a rapid growth in diaspore production per unit surface occurred over the successive study years (Fig. 13), as a result of an increase in the number of fruiting individuals in the population, and of fractions of older tussocks with a higher individual production. In population 2, a steady growth of diaspore production was observed only before and in 1972, whereafter a drop in production was seen — until the end of the investigations — as the population decreased. Subject to a low degree of variation was the production of diaspores in population 3 (Fig. 13), the number of caryopses produced by an average tussock and a collective fruit being relatively small (Fig. 12).

The real reproductiveness in the populations under study, as measured by the number of emerged seedlings (Fig. 12), was much lower than could be expected from the number of the

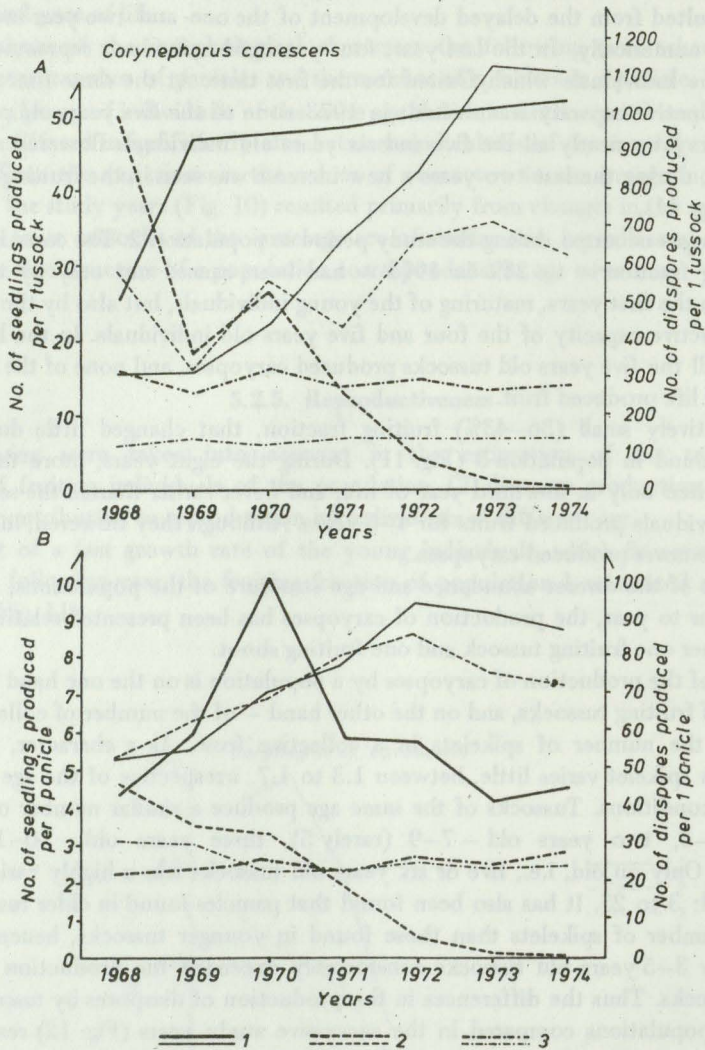


Fig. 12. Total fecundity (thin lines) and real reproductive index (thick lines) per one fruiting tussock (A) and one fruiting shoot (B) in populations 1, 2, 3

diaspores produced, and the variations in the individual years only to some extent corresponded to the variations in the overall fecundity. The highest reproductive index was recorded for population 1. Assuming that all the caryopses with germinating capacity germinate in the first year, for this population also the highest per cent germination was found: 16.25% in 1970. In population 2 a fall in the reproductive index and germinating capacity during the study years (from 8.7% in 1968 to 0.004% in 1974) took place, whereas the reproductive index of population 3 changed very little from year to year. Each year, 2.4 to 3.2% of the total number of diaspores produced in it germinated.

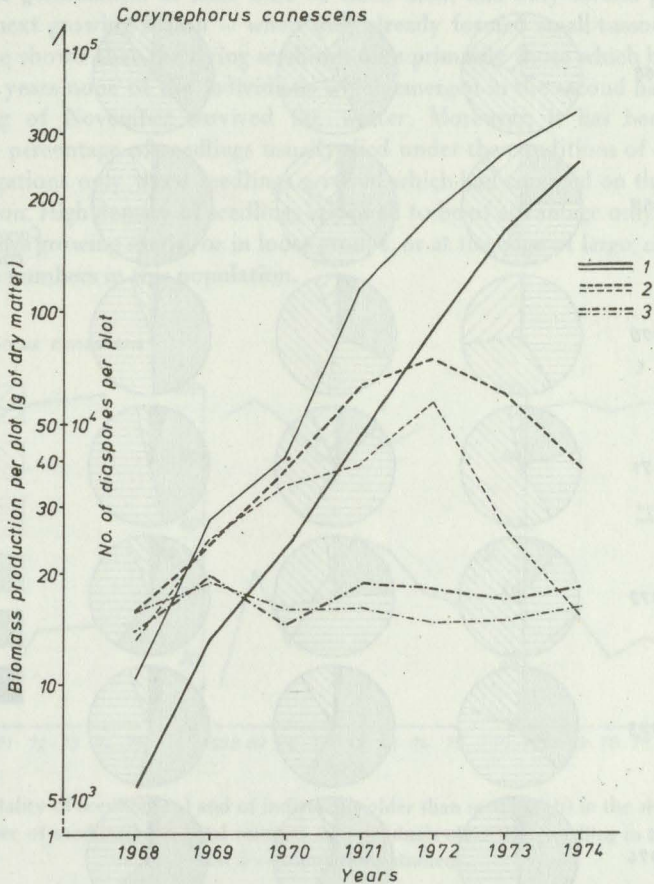


Fig. 13. Production of biomass (thick lines) and of diaspores (thin lines) in populations 1, 2, 3, in the study period

Noteworthy is the fact that in the laboratory 62 to 68.5% of the diaspores of each population germinated, irrespective of the age of the tussocks that produced them.

The contribution of different age individuals to the reproduction is shown in Figure 14. The diagrams represent the production of caryopses by individuals of different age, because under natural conditions it is difficult to estimate their contribution to the real reproductiveness. Because of the insignificant differences in the germinating capacity of the diaspores derived from tussocks of different age, it was possible to assume that the contribution to the real reproductiveness is the same as to the production of diaspores. From Figure 14 it follows that responsible for the main reproduction of the population are the three and four years old individuals, because of their high individual production. It is sufficient to note that an average three years old tussock produces 5–6 times as many diaspores as does a one year old tussock, and a four years old tussock – 10 times as many. Tussocks above four years of age produce the same number of diaspores as the one and two years old ones. Thus only with a considerable

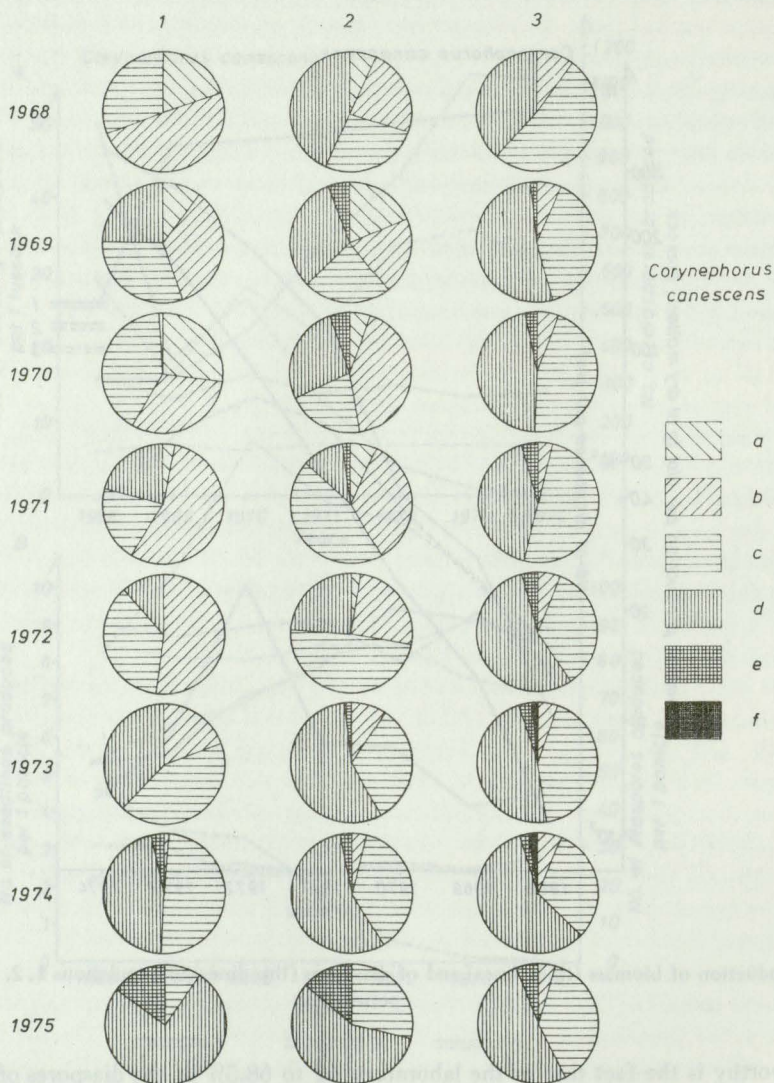


Fig. 14. Contribution to reproduction by individuals of different age

a – one year old, b – two years old, c – three years old, d – four years old, e – five years old, f – older than five years; 1, 2 and 3 – populations studied

numerical dominance of the one and two years old tussocks, as in population 1 in the period 1968–1972, could a dominance of the contribution of young tussocks to the reproductiveness be seen.

5.2.6. Mortality

The number of dying individuals in a population, and especially the percentage of the individuals that died every year, relative to those surviving, indicated a high mortality of the

populations of *C. canescens* (Fig. 15). The number of dying seedlings was very large; within two months from the germination at least 80% of them died, and only several per cent of them survived to the next growing season – when they already formed small tussocks. More precise observations have shown that the dying seedlings were primarily those which had emerged late; during the eight years none of the individuals which emerged in the second half of October, or at the beginning of November survived the winter. Moreover, it has been found that a particularly high percentage of seedlings usually died under the conditions of overcrowding: in very thick aggregations only those seedlings survived which had emerged on the first, or second day of germination. High density of seedlings appeared to be of advantage only in population 1; it was the seedlings growing singly, or in loose groups, or at the edge of large, close aggregations that died in large numbers in this population.

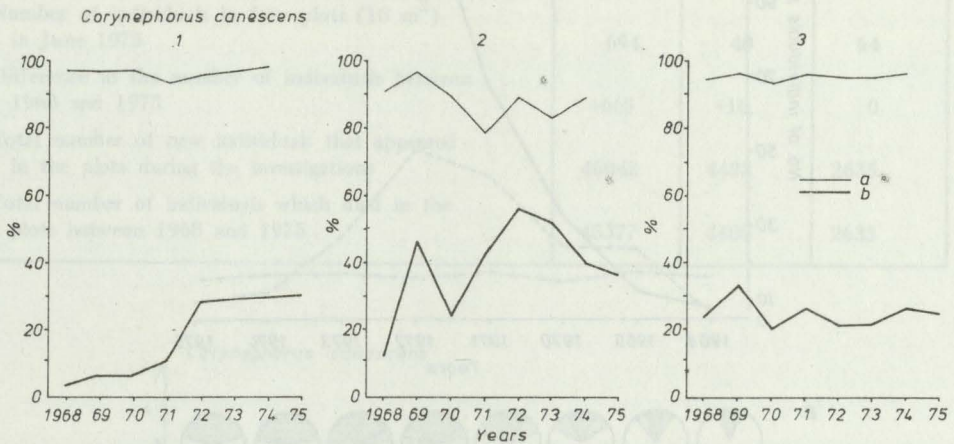


Fig. 15. Mortality of seedlings (a) and of individuals older than seedling (b) in the study years 100% – total number of seedlings and total number of individuals older than seedling in the given year; 1, 2 and 3 – populations studied

Figure 15 shows that the dying seedling fraction almost did not change from year to year, being very high in populations 1 and 3; greater variations, and at the same time a lower mortality were found in population 2.

The remaining individuals of the population died in much smaller numbers, especially those two, three and four years old. Beside the seedlings, mortality affected a comparatively large number of old individuals and one year old tussocks, especially those in high density aggregations. Mass mortality also occurred among one year old individuals of population 2 after 1972, regardless of the density.

The withering of old tussocks was much slower than that of the young ones; it sometimes lasted 3–4 years. It also happened that a half-dead tussock produced in the following year not only new vegetative shoots, but also inflorescences. However, such tussocks never fruited.

5.2.7. Abundance dynamics over a many years' period

In the estimation of the variations in numbers over a period of many years taken into account were the minimum levels of numbers in the fruiting periods of *C. canescens* in all the years. The variation curve (Fig. 16) is based on the average population density from 4 plots.

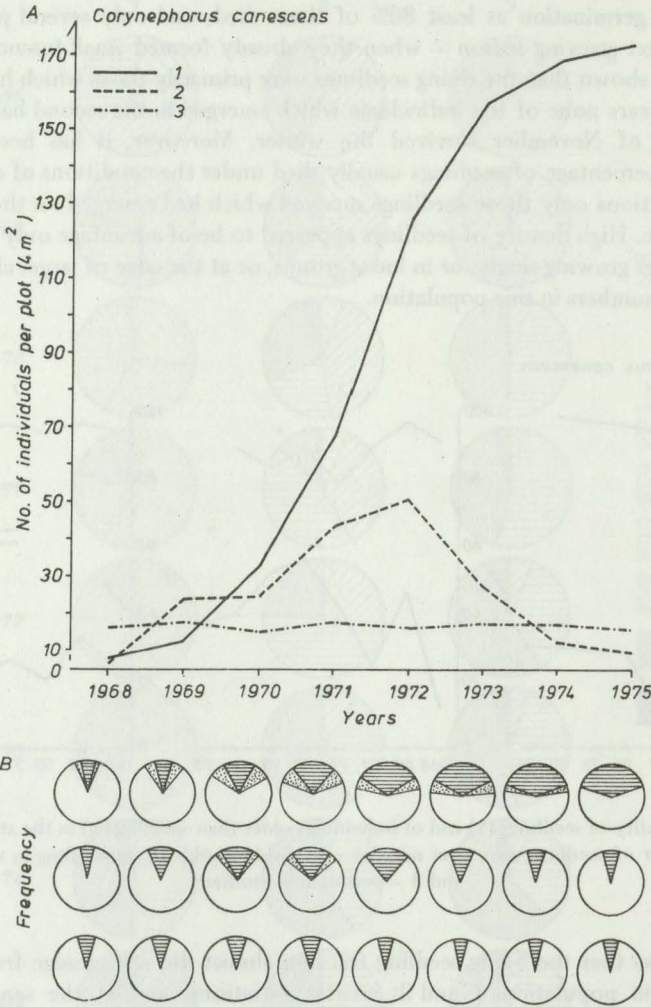


Fig. 16. Many years' abundance dynamics (A) and frequency variations (B) in plots during the study years. Shaded area - frequency during fruiting period, dotted area - per cent of plots occupied by seedlings exclusively; 1, 2, 3 - populations studied

It has been found that the type of the many years' dynamics, and the rate of changes in numbers were different in each of the populations compared (Table I). In population 1 a steady growth of the number of individuals was found. The corresponding curve resembles the S-shaped curve characterizing populations in the growing phase with limited supplies in the environment. In the many years' abundance dynamics of this population it is possible - on the basis of the curve - to distinguish a phase of positive acceleration (1968-1969), a logarithmic phase (1970-1973), and a negative acceleration phase (1974-1975). The steady net increase of the population (Fig. 17) resulted in an almost 25-fold increase in the abundance of the population within only eight years. In the same period, there was only a 5-fold increase in frequency

in the plots, so the real density in a plot increased at least six times. More than a half of the area remained unoccupied till the end of the investigations (cf. Fig. 8).

Table I. Abundance balance of three *Corynephorus canescens* populations during the study period

Parameters	Populations		
	1	2	3
Number of individuals in four plots (16 m ²) in June 1968	29	26	64
Number of individuals in four plots (16 m ²) in June 1975	694	40	64
Difference in the number of individuals between 1968 and 1975	+665	+16	0
Total number of new individuals that appeared in the plots during the investigations	46042	4422	2635
Total number of individuals which died in the plots between 1968 and 1975	45377	4408	2635

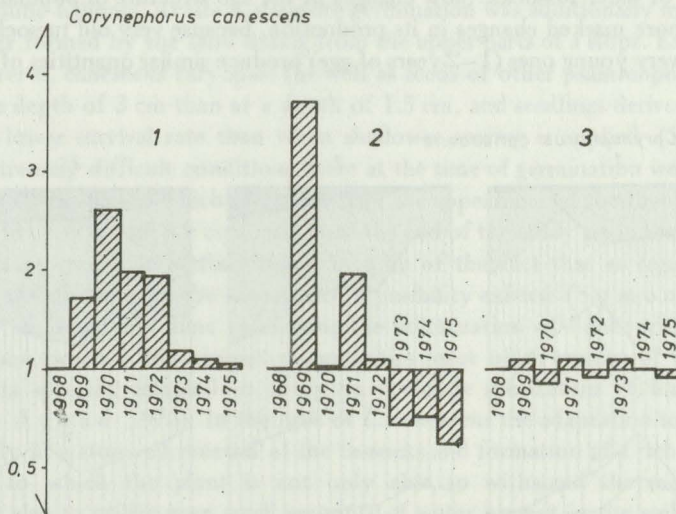


Fig. 17. Index of net increase of populations 1, 2, 3 in the successive study years (the unit of comparison is always the population abundance in the previous year)

The curve illustrating the course of changes in the abundance of population 2 is clearly one-peak curve (Fig. 16), both the growth and the decrease of numbers being fairly rapid (Fig. 17). The frequency in the plots changed in the same direction as the abundance, the frequency changes being statistically insignificant.

During the study period the level of numbers in population 3 was maintained in the state of a relative equilibrium (Figs. 16, 17). The small variations in numbers were statistically insignificant.

The population abundance dynamics observed in the plots proceeded in a similar way in the whole area of the community. This is indicated by the lack of significant differences between the density in the plots and in the remaining several quadrats, where similar numbers of individuals were found in the first study year.

5.2.8. Biomass production

The quantity of biomass produced is the resultant of the size of a population and its age composition. Individual production by *C. canescens* tussocks grew fast until the fourth year of life (inclusive) whereafter it rapidly decreased. Five years old tussocks did not produce more biomass than the two years old ones, whereas six years old tussocks produced much less than those in the first year of life. Tussocks of the same age in general produced similar quantities of biomass throughout the study period, regardless of the habitat conditions. Only in 1969 was the production lower on an average by 22% in all the populations. A considerable fall in the yearly biomass increments was also recorded for population 2 in the last 2 study years. Root production represented about 48% of the total production in the case of population 1, and about 42–43% – in the case of the remaining populations.

The many years' dynamics of biomass production by the populations studied (Fig. 13) was similar to the abundance dynamics. The rapid growth of the yearly biomass increments in population 1 resulted not only from a fast increase in numbers, but also from a steady increase in the proportion of older tussocks. Slow changes in the age structure of population 3 did not bring about any more marked changes in its production, because very old tussocks (6–7 years of age), as well as very young ones (1–2 years of age) produce similar quantities of biomass.

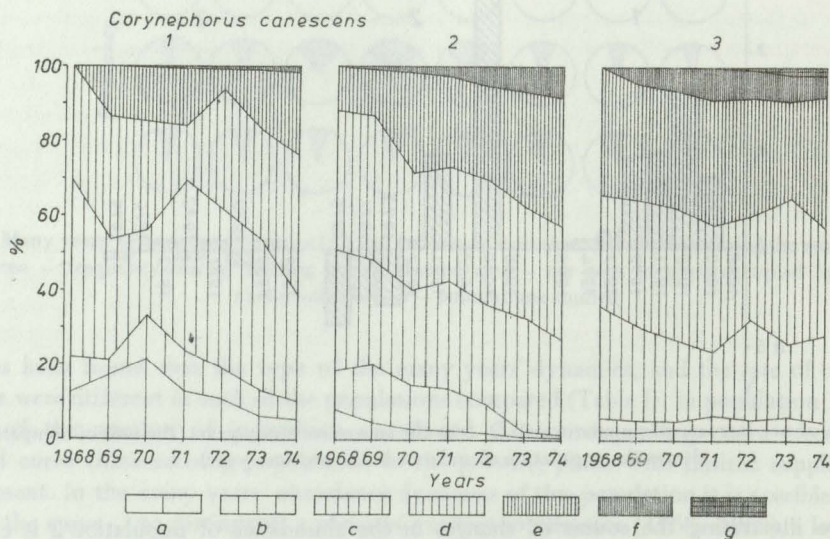


Fig. 18. Contribution of different-aged individuals to biomass production

a – seedlings, b – one year old individuals, c – two years old, d – three years old, e – four years old, f – five years old, g – older than five years; 100% – total biomass production in the given year by populations 1, 2, 3

The contribution to the total production of individuals of different age during the study years has been presented in Figure 18. In population 1, 50% of the biomass was for six years produced by young individuals: seedlings, one and two years old individuals; from 1972 on the proportion of older tussocks increased. Changes in population 2 followed a similar direction. The contribution to the production of biomass of the individuals of different age in population 3 varied slightly from year to year; at least 60% of the biomass was produced by three and four years old tussocks. With the years passing, there occurred an increase in the contribution of old individuals to the production of biomass.

6. DISCUSSION

The initial phase of sand colonization and dune overgrowing in the study area was relatively slow, especially at sites much exposed to the accumulation and deflation caused by the moving sand. Although the bare dune areas are of a secondary nature since they arose due to the destruction of the forest vegetation, the thick, in some places 1.5 m thick, raw sand layer, almost without humus (Symonides 1974), the deep level of ground waters (5–6 m acc. to Mrózek and Regel 1965), and a predominance of the fine-grained fraction in the sands, created conditions, similar to those in a desert, highly unfavourable to plant growth. Due to their poor permeability, fine-grained sands are, according to Bond (1968), one of the main causes of the poor germination of seeds, and thereby a slow growth of vegetation in extremely dry dune habitats. At site 1, diaspore germination was additionally made difficult by a too thick layer formed by the sand sliding from the upper parts of a slope. Experiments have shown that fewer *C. canescens* caryopses (as well as seeds of other psammophytes) germinate when sown at a depth of 3 cm than at a depth of 1.5 cm, and seedlings derived from a deeper sowing show a lower survival rate than when shallower sowing is applied (Symonides 1978a). The extremely difficult conditions there at the time of germination were no doubt the most important factor, due to which five years after the appearance of the first plants the cover at site 1 was as low as several per cent, and until the end of the study period no individual of a different species succeeded in settling there, in spite of the fact that as regards the specific composition of the diaspores in the sands, such a possibility existed (Symonides 1978b).

In extremely unfavourable dune conditions the colonization of dunes with plants usually takes a long time, whereas the pioneer communities most often consist of one, rarely two species of plants specially adapted to living on a mobile substratum (Chadwick and Dalke 1965, Ayad 1973). In the case of *C. canescens* the adaptation to living on sands consists primarily in a storeyed renewal of the tussocks and formation of a rich secondary root system, owing to which the plant is not only able to withstand the movement of the substratum, but also to utilize even small amounts of water present in the soil (Marshall 1965, 1967). J. Kobendza and R. Kobendza (1958) report that the total length of the secondary roots of *C. canescens* is 700–800 m. According to the measurements made by the author of the present paper, old tussocks of *C. canescens* found on poorly overgrown sands produce roots of a total length of up to 4900 m, although the vertical range of the longest roots in the sand is only 35 cm. The typically xeromorphic stem structure protects this species against losing too much water. Owing to this structure, transpiration can be almost completely stopped during dry weather, although when there is enough moisture in the sands, the

transpiration rate is fairly high (Rychnovská-Soudková 1961, Rychnovská and Květ 1963, Berger-Landefeldt and Sukopp 1965). Another valuable property of this pioneer plant is its very high production of diaspores and mass dissemination under favourable conditions, as a result of which it can colonize a dune within as short a time as 2–3 years (Kornaš 1972).

The first *C. canescens* tussocks which succeed in settling and holding-on on the moving substratum form specific microhabitats in their closest vicinity, which are more favourable for the settling of further individuals of the population. *C. canescens* tussocks stop the sand and protect the surface layers against overdrying, for this reason seedlings emerge primarily in their closest vicinity. Thus the aggregated structure forms from the beginning of the development of a pioneer population, and it does not change as it grows in numbers. Different results have been reported by Walter (1962), and MacArthur and Connell (1971). In extreme habitats, where one factor or a group of factors limited the growth of plants, the above authors found tendencies to an even spatial distribution, due to a negative interaction between individuals. Nor have the studies confirmed the view held by Chapman (1960) and Vasilevič (1969) that the more abundant the species, the more evenly it colonizes a space. However, the results of the studies agree with the findings of Greig-Smith and Chadwick (1965); they attribute the aggregated distribution of plants in semi-deserts and savannahs to the dissemination of seeds around parent individuals. In the case of *C. canescens*, the type of spatial structure of a population is to a large extent determined by the distribution of diaspores accumulated near the tussocks, or in local land depressions (Symonides 1978b), and by the higher survival rate of the seedlings growing in aggregations relative to those growing singly. Up to a certain level of density seedlings in aggregations more easily withstand being covered up with sand, but first of all they suffer much less from low temperatures in winter, to which *C. canescens* is not very resistant (Marshall 1967).

The aggregated structure of seedlings resulted in a fairly fast increase in the density of the aggregations, but, on the other hand, also in a rather poor efficiency of the fixing of sands over a wider area, two thirds of which on site 1 remained unfixed until the end of the investigations. This no doubt made difficult the settling of species less resistant to being covered-up. According to Chadwick and Dalke (1965), the lability of bare sands is a more important factor limiting the free settling of plants than is the shortage of nutrients. The views of the authors just named have been confirmed by the gradual enrichment in species of the community on site 2, where the sands became fixed within a short time by *Polytrichum piliferum* although they were as poor in nutrients as those on site 1. Areas where *Polytrichum piliferum* did not form compact turfs, and where its loose patches prevented the sand from being blown away by the wind and overdried, were gradually more and more abundantly colonized not only by herbaceous plants, but also by the seedlings of *Pinus sylvestris* and *Calluna vulgaris* (L.) Salisb. It was only the compact moss turfs that made further spreading of flowering plants difficult, mainly by retaining their diaspores and impeding the growth of seedlings. This brought about a change in the age structure, a rapid lowering in the reproductiveness, and consequently, a rapid fall in the abundance of the *C. canescens* population. A similar response was recorded for other species reproducing generatively. Populations of species reproducing vegetatively appeared to be much stronger in the competitive struggle against *P. piliferum*, in which a steady, gradual increase in numbers could be seen.

The expansion of *P. piliferum* was no doubt the main factor affecting the course of sand colonization, and the dynamics of the flowering plant populations on site 2. The moss has been found to be much more efficient in the fixing of moving dunes than was *C. canescens*. The

studies carried out by Marsh and Koerner (1972) indicate that *P. piliferum* can easily spread even under the conditions of a continuous covering-up with sand on steep slopes, provided they are relatively moist. The phase of *P. piliferum* dominance at site 2 was probably short, transitional. Already in 1974 the blowing away of the oldest parts of the turf, dry and crumbling, could be seen, and their replacement by flowering plants, primarily *Festuca psammophila*, *Koeleria glauca* and *Helichrysum arenarium*.

A different, in respect of the consequences, result of the interspecific competition was the high stability of numbers in population 3, even at a comparatively low density level. During the eight years' period only a slow "maturing" of the population could be seen manifested by an enrichment of the age structure with a group of individuals five, six and seven years old. The remainder of the population characteristics, relating to both the structure and function, were subject to only slight variations from year to year. Moreover, the structure of the age pyramid in the last study year, as well as the fraction of fruiting individuals, did not predict any quick changes in numbers in the next years. The low germination percentage and the mortality of seedlings, which was high every year, although their density was not high, and the environmental conditions were relatively good, indicate that the effect of the factors limiting the increase of a population is visible in the germination period and in the seedling phase, the basic limiting mechanism being the interspecific competition. A simple experiment has fully confirmed the supposition that the stability of a *C. canescens* population is maintained via a competitive action of the populations of *Festuca psammophila* and *Koeleria glauca*, coexisting with it. As a result of the removal of both "competitors", the following year already there was an increase in numbers and in the survival rate of seedlings of *C. canescens*. The competitive power of *F. psammophila* and *K. glauca* lies in their specific ability to retain moisture in the rhizosphere; they accumulate the moisture, in the form of compact envelopes of sand grains, along all their roots (Wilkoń-Michalska and Symonides 1974). If the areas of the two grass species overlap, the sands in the rhizosphere of *C. canescens* become overdried (Rychnovská-Soudková 1961). Rychnovská-Soudková (1961) has stressed the fact that because of the high rate root respiration in *C. canescens*, another factor eliminating this species at the later stages of dune overgrowing is a lowering of the air capacity of the soil, as a result of the accumulation of humus.

An analysis of the seasonal and the many years' dynamics of population 1 leads to the conclusion that the factors responsible for the level of density of a highly pioneer population change with the changing population density and habitat conditions. At the early stages of the development of a population, an increase in density reflects first of all some better changes in the habitat conditions (cf. Hayashi and Numata 1967, 1968). At the later stages, the effect is seen of the competition among the individuals of the population, the intrapopulation mechanisms becoming noticeable when the density level is still relatively low. Because of this, the steady growth of the net increment index was later on followed by a decrease in its value, and the tendency to limit the growth in numbers became stronger and stronger from year to year, in spite of the very high production of caryopses, better conditions for the growth of seedlings, and a fairly large free space, not occupied by the population till the end of the investigations. The tendency to stabilize the system at a comparatively low density level probably resulted from insufficient supplies of nutrients in the soil, which, according to Chandapillai (1970), is the most important factor making impossible the formation of thick communities on dunes.

With an increase in the density the competition among the seedlings was particularly strong, which has been discussed in detail in the previous papers (Symonides 1977, 1978a).

A further effect of the overcrowding was a retardation of the development of the juvenile individuals, a lowering of reproduction, and an increase in mortality, that is, reactions fairly common in the populations of many plant species (Rabotnov 1950, Harper 1967, Wilkoń-Michalska 1976, Falińska 1977, and many others).

Summing up the discussion on the variations in the density of the populations studied, it should be mentioned that the number of diaspores produced, and thereby the density of sowing have at the most a secondary effect on the density of a population; in none of the populations studied was a direct relationship found between the number of diaspores produced and the number of seedlings. Thus the density of the individuals that survive is determined independently (to a large extent) of the initial population density. A lack of such relationship in many plant species has been demonstrated by Yoda et al. (1963).

It may be as well to note that exogenic factors, abiotic and biotic, to a large extent limited the realization of the tremendous biotic potential of *C. canescens*. Particularly unfavourable for the reproduction is the interspecific competition; in the extreme conditions of site 1, but with no competitors – the efficiency of the population in the production of offspring was much higher than on site 2 and 3. The rapid growth of the reproductiveness in the experimental plots on site 3, after the tussocks of *F. psammophila* and *K. glauca* had been removed, indicates a low competitive power of *C. canescens*. In the case of *C. canescens*, competition brought about a clear shift of the ecological optimum (relative to the physiological one) which a population finds in habitats that are extremely unfavourable for other species. It may, therefore, be presumed that the ecological scale of *C. canescens* is much wider than indicated by the observation of its natural distribution. Competition plays an important role in the regulation of the abundance of plant populations, especially in phytocenoses with a complex structure. It also considerably narrows the tolerance limits of each species, as a result of which, many of them have two optima of growth: physiological and ecological (Zarzycki 1965, 1968).

To any changes in the environmental conditions *C. canescens* populations characteristically reacted almost exclusively by a reduction or an increase in the number of individuals, and to a lesser extent by a change in the rate of their growth. The least changing features were the following: size of tussocks of the same age, number of complex fruits, individual production of diaspores and of the biomass of the vegetative parts. It must be pointed here that according to the data in the literature (Marshall 1967), *C. canescens* tussocks can attain a much larger size, and, similarly, they can produce more caryopses than has been shown by the investigations here presented. This would indicate that the conditions in the study area are very unfavourable for the growth of *C. canescens*, both the physical habitat conditions (site 1) and the interspecific competition (sites 2 and 3) exerting an adverse influence.

Although the phytocenoses analysed were located near one another, the differences found in the structure, abundance, and in the abundance dynamics of three *C. canescens* populations indicate that they were ecologically different. They indicate also that individuals of one species occurring in different phytocenoses must be looked upon as forming different populations.

7. SUMMARY

The paper presents the results of studies concerned with sand colonization and development of initial communities on inland dunes, and with the population structure and dynamics of *Corynephorus canescens*, a pioneer plant of bare sands. The present studies are part of some wider-scope series, the aim of which was: (1) to analyse populational phenomena and processes in several psammophyte species under the conditions of

formation and succession of plant communities, (2) to study the course and the rate of the overgrowing of a dune with vegetation.

The investigations were carried out on a dune in the Toruń Basin in the years 1968–1975 (Fig. 1). The species composition, abundance, per cent cover, frequency, and the biomass of the populations of the individual species in each community were analysed in 10 permanent areas (256 or 100 m²) located on nearly bare sands, and within more or less thick psammophilic sods. In each area 4 plots were marked off (4 or 1 m²) to be used for detailed studies of the populations of one or several species belonging to the community. The scope of the study included: seasonal and many years' abundance dynamics, spatial structure, age structure, reproductiveness, mortality and biomass production.

Sand colonization, development of initial communities on inland dunes and the properties of *C. canescens* populations were investigated at sites 1, 2 and 3 (Fig. 1).

In the first study year, only 7% of site 1 was covered with *Corynephorus canescens* and *Spergula vernalis*. During the eight years' observation period the growth of the initial vegetation proceeded only towards an increase in numbers of both populations, but the number of species did not increase. The two species fixed about 70 m² of sands, and there was an 86-fold increase in their biomass (Fig. 3). The main role in the fixing of the sands was played by *C. canescens*. In spite of the extreme habitat conditions, there occurred a 40-fold increase in the number of individuals in the population of this species (Fig. 16 A); the frequency increased slightly in both the plots and study areas (Fig. 16 B), mainly due to the aggregated spatial structure of the population (Fig. 8). The population growth rate was the resultant of the short pregenerative period (Fig. 9) and high indices of general fecundity and reproductiveness (Fig. 12). Each year a high mortality, above 90%, especially of the seedlings (Fig. 15) was recorded.

At the beginning of the studies, the degree of sand fixing, the specific composition, and the population size of site 2 were similar to those on site 1. However, the moister sands of the former created better conditions for plant growth (Symonides 1974). During the study period, the floristic list of the community increased by 12 species, but an increase in the total number of individuals of flowering plants was only recorded till the year 1972 (Fig. 4). The rapid fall in their numbers in the next years was caused by a rapid spreading of *Polytrichum piliferum*, whose dense turf made impossible the growth of the seedlings and development of juvenile individuals. In *C. canescens* populations fast age-structure changes took place, indicating a decline of the population (Fig. 9), decrease in the number of seedlings (Figs. 7, 12), lowering of the production of biomass and diaspores (Fig. 13), mas withering of tussocks.

Site 3 was selected for studies of the dynamics of the initial communities, and it represented a poor patch of *Spergulo-Corynephorum* on sands, 35% of which was fixed by the populations of 12 psammophyte species. The changes observed in the study period concerned: (1) number of species (three new species arrived, one retreated), (2) number of individuals (an increase by 17%), (3) quantitative relations between the populations of the different species (a fast growth in number of *Festuca psammophila* and *Koeleria glauca*; a decrease of *Spergula vernalis*), (4) cover (an increase by 21.9%) and (5) biomass (a growth by 48%) (Fig. 5). Throughout the study period *C. canescens* population retained all the features of a stabilized population (Figs. 7, 9–18).

Interspecific competition was found to limit the free growth of *C. canescens* population more efficiently than the physical conditions of the habitat.

8. POLISH SUMMARY

W pracy przedstawiono wyniki badań dotyczących zasiedlania piasków i rozwoju inicjalnych zbiorowisk na wydmach śródlądowych oraz struktury i dynamiki populacji *Corynephorus canescens*, pionierskiej rośliny nagich piasków. Badania te są częścią szerszych studiów, których celem było: 1) analiza zjawisk i procesów populacyjnych u kilku gatunków psammofitów w warunkach tworzenia się i sukcesji zbiorowisk roślinnych, 2) zbadanie przebiegu i tempa zarastania wydmy.

Badania przeprowadzono w latach 1968–1975 na wydmie w Kotlinie Toruńskiej (rys. 1). Na 10 stałych powierzchniach (256 lub 100 m²), zlokalizowanych zarówno na prawie nagich piaskach, jak też w obrębie mniej lub bardziej zwartych muraw psammofilnych, analizowano skład gatunkowy, liczebność, pokrywanie, frekwencję i biomasę populacji poszczególnych gatunków każdego zbiorowiska. W obrębie powierzchni wytyczono po 4 poletka (4 lub 1 m²) do szczegółowych badań populacyjnych jednego lub kilku gatunków wchodzących w skład zbiorowiska. Zakres tych badań obejmował: sezonową i wieloletnią dynamikę liczebności, strukturę przestrzenną, strukturę wiekową, rozrodczość, śmiertelność i produkcję biomasy.

Zasiedlanie piasków i rozwój inicjalnych fitocenzoz na wydmach śródlądowych oraz właściwości populacji *C. canescens* badano na powierzchniach 1, 2 i 3 (rys. 1).

Powierzchnia 1 była pokryta w pierwszym roku badań zaledwie w 7% przez *Corynephorus canescens* i *Spergula vernalis*. W ośmioletnim okresie obserwacji rozwój inicjalnej roślinności przebiegał wyjątkowo w kierunku zwiększenia liczebności obu populacji, nie wzrosła natomiast liczba gatunków. Oba gatunki utrwaliły ok. 70 m² piasków, zaś ich biomasa wzrosła ponad 86 razy (rys. 3). Główną rolę w ustalaniu piasków spełniał *C. canescens*. Mimo ekstremalnych warunków siedliskowych stwierdzono w populacji tego gatunku czterdziestokrotny wzrost liczby osobników (rys. 16 A); frekwencja w obrębie poletek oraz na powierzchni badawczej zwiększyła się nieznacznie (rys. 16 B), przede wszystkim wskutek skupiskowej struktury przestrzennej populacji (rys. 8). Tempo wzrostu liczebności populacji wynikało z krótkiego okresu przedrodzowego (rys. 9) oraz wysokich wskaźników płodności ogólnej i rozrodczości (rys. 12). Śmiertelność, zwłaszcza siewek, była wysoka w każdym roku i przekraczała 90% (rys. 15).

Stopień utrwalenia piasków oraz skład gatunkowy i liczebność populacji na powierzchni 2 w momencie rozpoczęcia badań kształtowały się podobnie jak na powierzchni 1. Nieco wilgotniejsze piaski stwarzały tu jednak korzystniejsze warunki dla rozwoju roślinności (Symonides 1974). W okresie badań lista florystyczna zbiorowiska wzbogaciła się o 12 gatunków, jednak wzrost ogólnej liczby osobników roślin kwiatowych występował tylko do 1972 r. (rys. 4). Szybki spadek ich liczebności w następnych latach wywołany był gwałtownym rozprzestrzenieniem się *Polytrichum piliferum*, którego zwarte darnie uniemożliwiały wzrost siewek i rozwój osobników młodocianych. W populacji *C. canescens* stwierdzono szybkie zmiany w strukturze wieku, wskazujące na wycofywanie się populacji (rys. 9), spadek liczby siewek (rys. 7, 12), obniżenie produkcji biomasy i diaspor (rys. 13), masowe zasychanie kęp.

Do badań dynamiki inicjalnych zbiorowisk wyznaczono powierzchnię 3, reprezentującą ubogi płat *Spergulo-Corynephorum*, na piaskach ustalonych w 35% przez populację 12 gatunków psammofitów. W okresie badań zmiany dotyczyły: 1) liczby gatunków (przybyły trzy nowe, jeden wycofał się), 2) liczby osobników (wzrost o 17%), 3) stosunków liczebności pomiędzy populacjami poszczególnych gatunków (szybki wzrost liczebności *Festuca psammophila* i *Koeleria glauca*, spadek *Spergula vernalis*), 4) pokrywania (wzrost o 21,9%) i 5) biomasy (wzrost o 48%) (rys. 5). Populacja *C. canescens* w okresie badań zachowała wszystkie cechy populacji ustabilizowanej (rys. 7, 9–18).

Czynnik konkurencji międzygatunkowej skuteczniej ogranicza swobodny rozwój populacji *C. canescens* niż fizyczne warunki siedliska.

9. REFERENCES

1. Ayyad M. A. 1973 — Vegetation and environment of the western Mediterranean coastal land of Egypt. I. The habitat of sand dunes — *J. Ecol.* 61: 509–523.
2. Berger-Landefeldt U., Sukopp H. 1965 — Zur Synökologie der Sandtrockenrasen, insbesondere der Silbergrasflur — *Verh. bot. Ver. Brandenb.* 102: 41–98.
3. Bond R. D. 1968 — Waterrepellent sands (In: 9th International Congress of Soil Science, Adelaide, Australia 1968) — Halstead Press, Sydney, I: 339–347.
4. Chadwick H. W., Dalke P. D. 1965 — Plant succession on dune sands in Fremont county, Idaho — *Ecology*, 46: 765–780.
5. Chandapillai M. M. 1970 — Variation in fixed dune vegetation at Newborough Warren, Anglesey — *J. Ecol.* 58: 193–201.
6. Chapman V. J. 1960 — Salt marshes and salt deserts of the world — Leonard Hill Books, London, 392 pp.
7. Falińska K. 1977 — Strategia i taktyka reprodukcyjna populacji roślinnych [Reproduction strategy and tactics of plant populations] — *Wiad. ekol.* 23: 229–257.
8. Greig-Smith P., Chadwick M. J. 1965 — Data on pattern within plant communities. III. *Acacia-Capparis* semidesert scrub in the Sudan — *J. Ecol.* 53: 465–474.
9. Greń J. 1974 — Statystyka matematyczna: modele i zadania [Mathematical statistics: models and exercises] — Państwowe Wydawnictwo Naukowe, Warszawa, 362 pp.
10. Harper J. L. 1967 — A Darwinian approach to plant ecology — *J. Ecol.* 55: 247–270.
11. Hayashi J., Numata M. 1967 — Ecology of pioneer species of early stages in secondary succession. I — *Bot. Mag., Tokyo*, 80: 11–22.
12. Hayashi J., Numata M. 1968 — Ecology of pioneer species of early stages in secondary succession. II. The seed production — *Bot. Mag., Tokyo*, 81: 55–66.
13. Kobendza J., Kobendza R. 1958 — Rozwiewane wydmy Puszczy Kampinoskiej [Winnowed

- dunes in Kampinos Forest] [In: Wydmny śródlądowe Polski (Inland dunes of Poland). I, Ed. R. Galon] – Państwowe Wydawnictwo Naukowe, Warszawa, 95–171.
14. Kornaś J. 1972 – Zespoły wydm nadmorskich i śródlądowych [Associations of coastal and inland dunes] [In: Szata roślinna Polski (The vegetation of Poland). I, Eds. W. Szafer, K. Zarzycki] – Państwowe Wydawnictwo Naukowe, Warszawa, 303–309.
 15. MacArthur R. H., Connell J. H. 1971 – Biologia populacji [The biology of populations] – Państwowe Wydawnictwo Rolnicze i Leśne, Warszawa, 232 pp.
 16. Marsh W. M., Koerner J. M. 1972 – Role of moss in slope formation – *Ecology*, 53: 489–493.
 17. Marshall J. K. 1965 – *Corynephorus canescens* (L.) Beauv. as a model for the *Ammophila* problem – *J. Ecol.* 53: 447–463.
 18. Marshall J. K. 1967 – *Corynephorus canescens* (L.) Beauv. – *J. Ecol.* 55: 207–220.
 19. Mrózek W., Regel S. 1965 – Mapa hydrograficzna Polski [Hydrographical map of Poland], 1:500000 – Wydawnictwa Instytutu Geografii PAN, Warszawa.
 20. Oktaba W. 1966 – Elementy statystyki matematycznej i metodyka doświadczalnictwa [Elements of mathematical statistics and methodology of experimentation] – Państwowe Wydawnictwo Naukowe, Warszawa, 310 pp.
 21. Rabotnov T. A. 1950 – Žiznennyj cikl mnogoletnich trawjanistych rastenij v lugovych cenzach – *Geobotanika*, 3: 7–204.
 22. Rychnovská M., Květ J. 1963 – Water relations of some psammophytes with respect to their distribution (In: The water relations of plants, Eds. A. J. Rutter, F. H. Whitehead) – Oxford, 190–198.
 23. Rychnovská-Soudková M. 1961 – *Corynephorus canescens* (L.) Beauv. (Physiologisch-ökologische Studie einer Pflanzenart) – *Rozpr. čsl. Akad. Věd*, 71: 1–84.
 24. Symonides E. 1974 – Populations of *Spergula vernalis* Willd. on dunes in the Toruń Basin – *Ekol. pol.* 22: 379–416.
 25. Symonides E. 1977 – Mortality of seedlings in natural psammophyte populations – *Ekol. pol.* 25: 635–651.
 26. Symonides E. 1978a – Effect of seed size, density and depth of sowing on the germination and survival of psammophyte seedlings – *Ekol. pol.* 26: 123–139.
 27. Symonides E. 1978b – Numbers, distribution and specific composition of diaspores in the soils of plant association *Spergulo-Corynephorum* – *Ekol. pol.* 26: 111–122.
 28. Symonides E. (in press a) – The structure and population dynamics of psammophytes on inland dunes. II. Loose-sod populations – *Ekol. pol.* 27.
 29. Symonides E. (in press b) – The structure and population dynamics of psammophytes on inland dunes. III. Populations of compact psammophyte communities – *Ekol. pol.* 27.
 30. Symonides E. (in press c) – 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.
 31. Traczyk T. 1967 – Propozycja nowego sposobu oceny produkcji runa [A proposed new way of estimating the production of the forest herb layer] – *Ekol. pol.* B, 13: 241–247.
 32. Vasilevič V. I. 1969 – Statističeskie metody v geobotanike – Akad. Nauk SSSR, Leningrad, 230 pp.
 33. Walter H. 1962 – Die Vegetation der Erde in ökologischer Betrachtung. Vol. I. Die tropischen und subtropischen Zonen – Gustav Fischer Verlag, Jena, 538 pp.
 34. Wilkoń-Michalska J. 1976 – Struktura i dynamika populacji *Salicornia patula* Duval-Jouve [Structure and dynamics of the populations of *Salicornia patula* Duval-Jouve] – Uniwersytet Mikołaja Kopernika, Rozprawy, Toruń, 156 pp.
 35. 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) – *Fragm. flor. geobot.* 20: 497–528.
 36. Yoda K., Kira T., Ogawa H., Hozumi K. 1963 – Self-thinning in overcrowded pure stands under cultivated and natural conditions – *J. Inst. Polytech. Osaka Cy Univ. (Biology)*, 14: 107–129.
 37. 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.
 38. Zarzycki K. 1968 – Eksperymentalne badania zdolności konkurencyjnej roślin leśnych [Experimental investigation of competition between forest herbs] – *Acta Soc. Bot. Pol.* 37: 393–411.
 39. Zieliński R. 1972 – Tablice statystyczne [Statistical tables] – Państwowe Wydawnictwo Naukowe, Warszawa, 386 pp.