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MORTALITY OF SEEDLINGS IN NATURAL PSAMMOPHYTE POPULATIONS

ABSTRACT: Seedling mortality in natural populations of annual, biennial and perennial psammophyte species was investigated for seven years. The mortality of seedlings was found to vary little from year to year, and to be dependent primarily on the length of the life cycle and mode of reproduction of the particular species. The largest percentage of dead seedlings was recorded for the populations of perennial species, capable of vegetative propagation. A close (in general) relationship was found between the mortality of seedlings and their density. In a high-density population the most likely to survive were those seedlings which were the first to appear in the population.

Contents

1. INTRODUCTION

Many studies concerned with the survival of individuals in a population have proved that the highest mortality is peculiar to the early life stages of plants, and that as the age of the plants advances, there occurs a clear decrease in their mortality. The mortality of juvenile individuals, and of seedlings in particular, is one of the important population density controlling factors (Palmblad 1968) which as a rule attains a considerable level. This fact has been known for a long time and has been mentioned in many ecological papers (Rabotnov 1950, 1960, 1970, Braun-Blanquet 1951, Sukačev 1953, Knapp 1954, Zarzycki 1965a, 1965b, Mathews and Westlake 1969, Ross and Harper 1972, and many others).

Mortality of seedlings, often in large numbers, sometimes coming up to 99% of their total number, may be caused by many factors, both abiotic and biotic.

In connection with the studying of the mortality of juvenile individuals the following question arises: "Which seedlings of a population survive?" Morozow (1953) and Sukačev (1953) attribute an important role to the individual variation of seedlings, due to which there are weaker and stronger individuals at the beginning of their life. It has been also found that in di-specific and in multi-specific communities of much importance may be the sequence of appearance of the seedlings (Ross and Harper 1972).

In spite of the fact that there is a relatively large amount of data on the various aspects of the commonly occurring high mortality of seedlings, the problem is far from being known well, and it no doubt deserves attention. There is a lack of studies that would simultaneously analyze the influence of several factors on the magnitude and rate of seedling mortality in a population, and studies that would simultaneously take into account species differing in their biological properties.

The present paper presents some results from detailed studies, carried on for several years, on the mortality and survival of seedlings in selected populations of psammophytes. The aims of the studies were the following:

1. to determine the magnitude of mortality of the seedlings of species differing by their biological properties under similar habitat and climatic conditions;
2. to compare the seedling mortality rates in populations of species differing in the length of their life cycle;
3. to establish the interrelationship between the density of seedlings and their survival under different habitat and climatic conditions;
4. to analyze the mortality of seedlings in years differing by the course of weather phenomena;
5. to demonstrate a relationship between the sequence of appearance of the seedlings and their survival in one-species systems;
6. to determine the effect of adult individuals on the survival of seedlings in populations of polycyclic species.

The selection of psammophyte plants for studying the above problems was suggested primarily by methodical reasons. The identification and counting of seedlings in dune vegetation patches which are poor floristically and of a low degree of density was fairly easy. Relatively easy also was it to select suitable observation sites: to study the mortality within one population and one generation of individuals, within one population of a complex age structure, and finally, in di-specific and multi-specific systems.

The studies were carried out on a dune in the Basin of Toruń in the years 1968–1974. A detailed description of the climate, habitats and vegetation of the study area can be found in the paper by Symonides (1974a).

2. OBJECTS OF STUDY AND METHODS

The following species were selected for the study: annuals: *1 – Cerastium semidecandrum* L., *2 – Androsace septentrionalis* L., *3 – Plantago indica* L., *4 – Trifolium arvense* L., *5 – Spergula vernalis* Willd.; biennials: *6 – Jasione montana* L., *7 – Tragopogon heterospermus* Schweigg.; perennials: *8 – Corynephorus canescens* (L.) P. B., *9 – Festuca duriuscula* L., *10 – Koeleria glauca* (Schkuhr) DC., *11 – Scleranthus perennis* L.

Observations were carried out every 3–5 days (in early spring – every day) in a total of 24 plots each of 1 m^2 in area, in four replications per species. They were located in patches of five plant associations: *Spergulo-Corynephoretum* (species *5*, *8*), *Festuco-Koelerietum glaucae* (here two observation areas had been set up each consisting of four plots; in one of them species *2* and *4* were studied, and in the other one, species 7 and *10*), *Festuco-Armerietum* (species *1*, *9*), *Festuco-Thymetum serpylli* (species *6*, *11*) and *Corispermo-Plantaginetum indicae* (species *3*). Each field was divided into 100 equal unit squares, which made it easy to count the seedlings that appeared and those that died. In the case of very strongly compact clumps of *Corynephorus canescens* and *Cerastium semidecandrum* seedlings, where direct counting of seedlings was impossible, an estimative method was used. For this purpose, 10 squares, densely overgrown with seedlings, each of the size 5 × 5 cm, were cut out outside the plots, and the seedlings were counted. Knowing the average seedling density per unit area, it was possible to estimate the number of seedlings per a plot square. Seedlings that appeared during the first days (or ten-days' periods) of germination were marked with coloured sticks in the field, or mapped down on a distribution chart. Such marking was not made in the first and in the last years of investigation.

To establish the effect of adult individuals on the survival of seedlings in populations of polycyclic species, in the last two years of investigation simple experiments were carried out. The experiments consisted in the removal of all adult individuals from a half of the study plots and of an appropriate number of the seedlings so as to have in each plot at least 6–8 squares of the same density.

The results of the observation were analyzed statistically, using the appropriate calculation methods and tests taken from the textbooks by Oktaba (1966) and Greń (1974). Statistical conclusions were always based on 0.95 confidence limit.

The meteorological data used in the interpretation of some of the results were obtained from the Institute of Meteorology and Water Management at Toruń-Wrzosy.

3. RESULTS

3.1. Seedling mortality during the investigation period

The starting point in mortality calculations (100%) was always the total number of seedlings of a species which appeared in the study plots during the growing season. As the germination process was spread over a certain period of time, and so was the mortality of seedlings which ran in parallel with it, this total considerably exceeded the maximum number of seedlings determined at a particular observation date. The only exception was the seedlings of *Cerastium semidecandrum* for which 100% appearance in as short a time as 5–7 days was recorded.

Figure 1 presents the average mortality rates of all the species, calculated on the basis of the studies that lasted seven years.

The results indicate that the mortality of seedlings was high in each population, as it exceeded 50% of the total number of seedlings. Moreover, it has been found that the annuals, and especially the early–spring ephemers (*Cerastium semidecandrum* and *Androsace septentrionalis*) showed a much higher per cent survival of seedlings than did the perennials; a particularly high seedling mortality was recorded for the grass species capable of vegetative propagation (*Koeleria glauca* and *Festuca duriuscula*). The differences, analyzed by means of

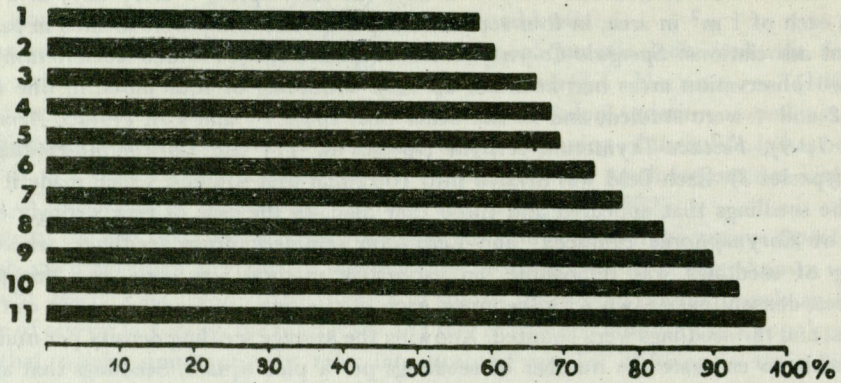

Fig. 1. Mean mortality of seedlings expressed as a percentage of their total number
Annual species: *1 – Cerastium semidecandrum, 2 – Androsace septentrionalis, 3 – Plantago indica, 4 – Trifolium arvense, 5 – Spergula vernalis;* biennial species: *6 – Tragopogon heterospermus, 7 – Jasione montana;* perennial species: *8 – Scleranthus perennis, 9 – Corynephorus canescens, 10 – Koeleria glauca, 11 – Festuca duriuscula*

the significance U test (Oktaba 1966), between the fraction of individuals which died in annual species populations, and the fraction of individuals which died in the populations of perennial species appeared to be significant even at the 0.1% error risk.

3.2. Seedling mortality at different life stages

Because the duration of the seedling phase varies with the species and from year to year (Fig. 2), to be able to compare the rate and the course of seedling mortality, the total length of

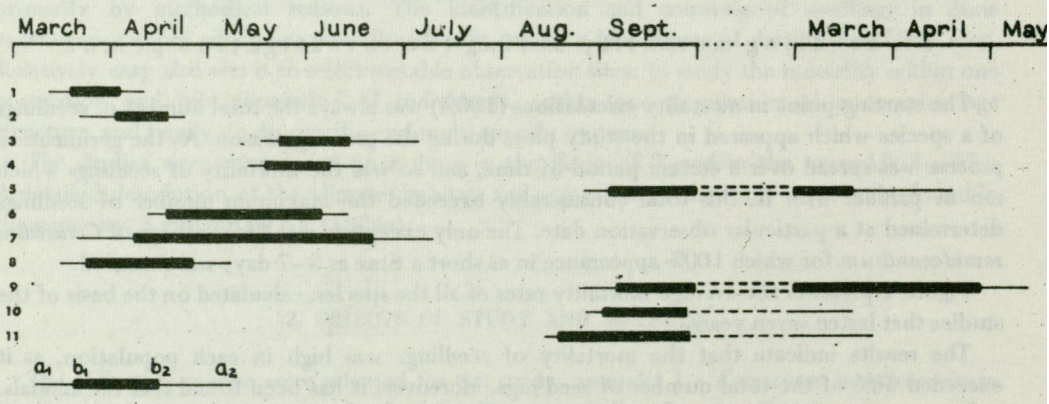

Fig. 2. Duration of seedling phase
a_1–a_2 – absolute dates of beginning and end of the phase in the years 1968–1974, b_1–b_2 – average dates of beginning and end of the seedling phase in the years 1968–1974. Species *1–11* as in Figure 1

this phase was assumed as 1 and was subsequently divided into five periods. At the end of each of the periods distinguished the per cent mortality was calculated relative to the total number of dead seedlings of the particular population. In the case of the populations of *Spergula vernalis* and *Corynephorus canescens*, the fifth period was longer than the four periods preceding it, and it comprised the winter months as well.

The phase began with the appearance of the first seedlings in a population; the date at which at least 60% of the seedlings had passed on to the next growth stage was adopted as the end-date of the phase.

The results have been presented in Figure 3. By using the variance analysis test, after a previous transformation of the empirical data according to the formula: $\varphi = 2 \arcsin \sqrt{p}$,

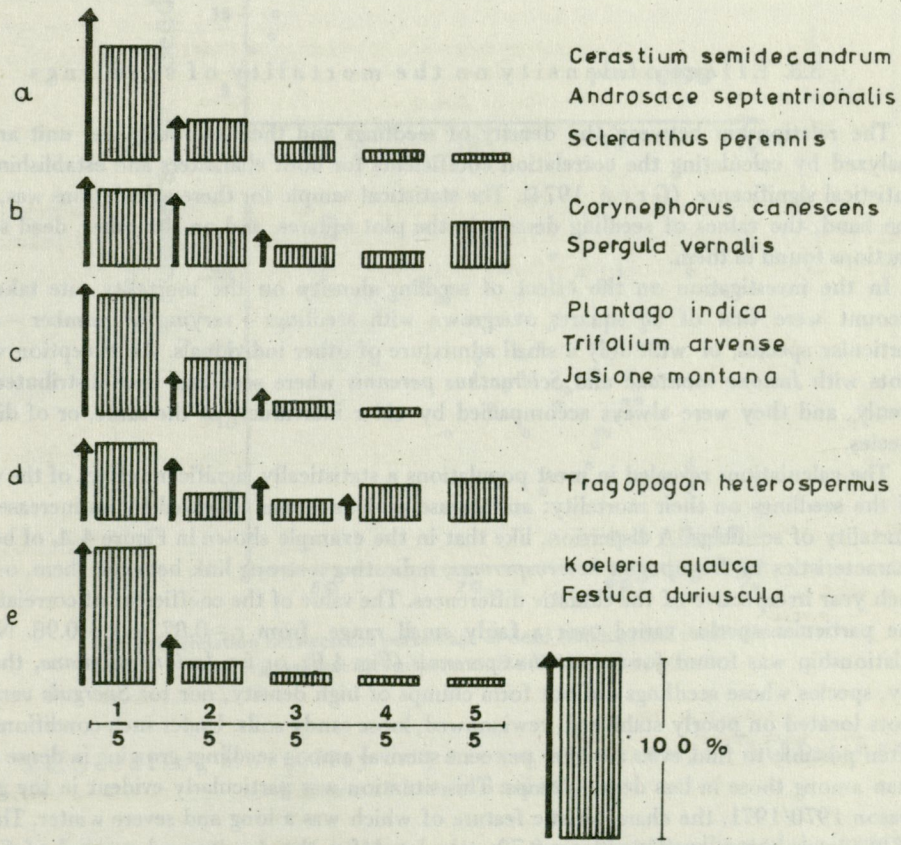

Fig. 3. Percentage of sprouted (arrows) and dead (bars) seedlings in individual periods of the seedling phase of the plant species under study

100% – total number of sprouted seedlings (arrows) and of dead (bars), 1/5–5/5 – total duration of the seedling phase, *a–e* – are used as indications in the text

where: p is the size of the fraction (Zieliński 1972)[1], a comparison was made of: (1) mortality fractions of each species in the particular periods of the phase of a seedling, (2) dying seedling fractions of the same species in the same period in different study years, (3) dying seedling fractions of different species in the same periods of each study year. In Figure 3 all the species with a similar seedling mortality course have been presented jointly. On account of the statistically insignificant differences between the mortality fractions in the corresponding periods of individual years, the data shown in Figure 3 represent average values for the seven-years' investigation period.

As indicated by the results, the rate of seedling mortality varied from species to species, being always the highest in the first period of the seedling phase. Except for *Spergula vernalis*, *Corynephorus canescens* and *Tragopogon heterospermus*, seedling mortality clearly dropped in the later periods, and there was no mortality at all in *Plantago indica*, *Trifolium arvense* and *Jasione montana*. Noteworthy also was a considerable coincidence of: mass appearance of seedlings, and their dying in large numbers (cf. Figure 3 – *a*, *c*, *e*).

3.3. Effect of density on the mortality of seedlings

The relationship between the density of seedlings and their mortality per unit area was analyzed by calculating the correlation coefficients for both characters and establishing their statistical significance (Greń 1974). The statistical sample for these calculations was, on the one hand, the values of seedling density in the plot squares, and on the other, dead seedling fractions found in them.

In the investigation on the effect of seedling density on the mortality rate taken into account were first of all squares overgrown with seedlings – varying in number – of one particular species, or with only a small admixture of other individuals. An exception was the plots with *Jasione montana* and *Scleranthus perennis* where seedlings were distributed fairly evenly, and they were always accompanied by older individuals of the same, or of different species.

The calculations revealed in most populations a statistically significant effect of the density of the seedlings on their mortality: an increase in density was followed by an increase in the mortality of seedlings. A dispersion, like that in the example shown in Figure 4 *A*, of both the characteristics in *Tragopogon heterospermus*, indicating a strong link between them, occurred each year irrespective of the climatic differences. The value of the coefficient of correlation for the particular species varied over a fairly small range, from $r = 0.87$ to $r = 0.98$. No such relationship was found for *Scleranthus perennis* (Fig. 4 *B*), or for *Jasione montana*, that is to say, species whose seedlings did not form clumps of high density, nor for *Spergula vernalis* in plots located on poorly stabilized, rewinnowed, loose sandy soils. Under such conditions it was often possible to find even a higher per cent survival among seedlings growing in dense clumps than among those in less dense clumps. This situation was particularly evident in the growing season 1970/1971, the characteristic feature of which was a long and severe winter. The value of the correlation coefficient, $r = 0.79$, calculated for the density and survival of *Spergula vernalis* seedlings in this season, clearly indicated a positive effect of higher densities.

[1] This transformation was used in all those tests in which fractions of dying or surviving seedlings were compared.

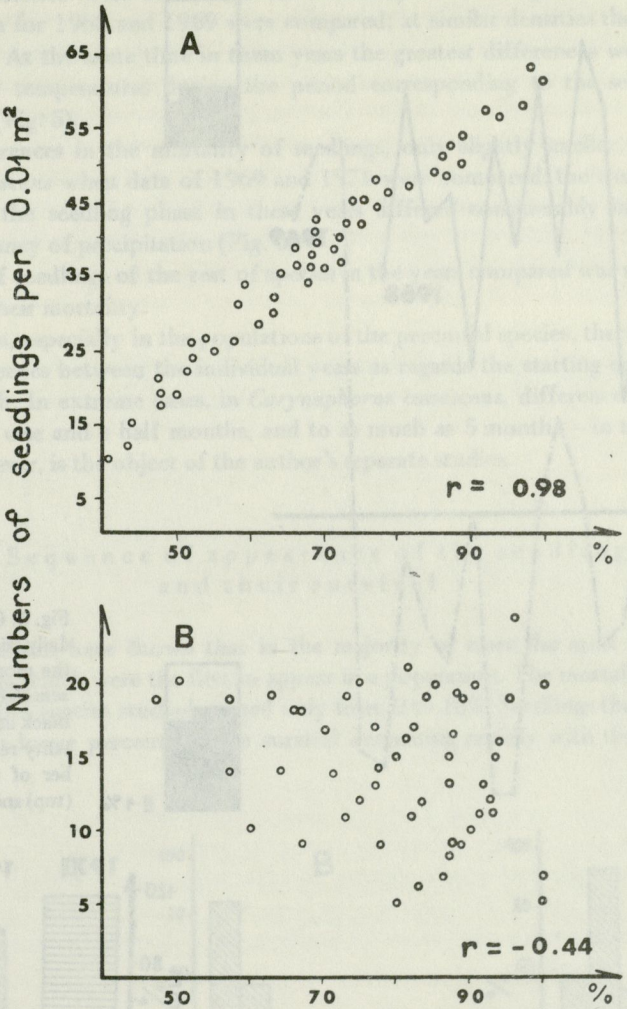

Fig. 4. Correlation between the percentage of dead seedlings and seedling density
A – Tragopogon heterospermus, B – Scleranthus perennis

3.4. Seedling mortality in years most strongly differing by weather conditions

To prove the significance of the differences in the mortality of seedlings of the investigated species, in individual years and irrespective of their density, the extreme – during the study period – values of seedling mortality in squares of equal, or similar number of grown seedlings, were compared. The null hypothesis of the lack of differences between the mean values of dead seedling fractions at similar density was verified by Student's *t*-test (Oktaba 1966).

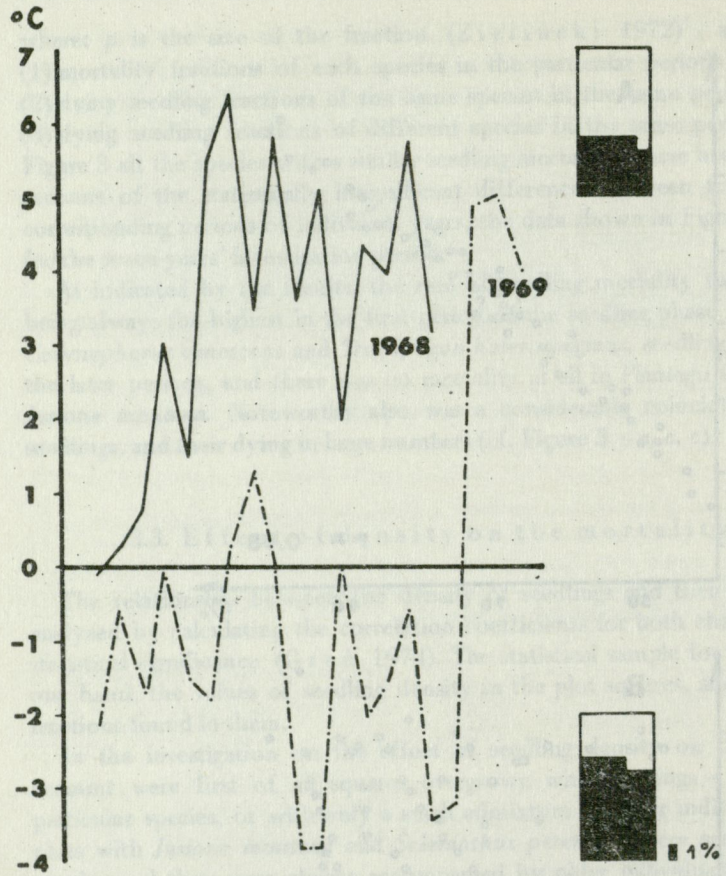

Fig. 5. Course of minimum daily air-temperatures and the mortality of *Cerastium semidecandrum* seedlings Black areas – per cent mortality relative to total number of seedlings in 1968 (top) and in 1969 (bottom)

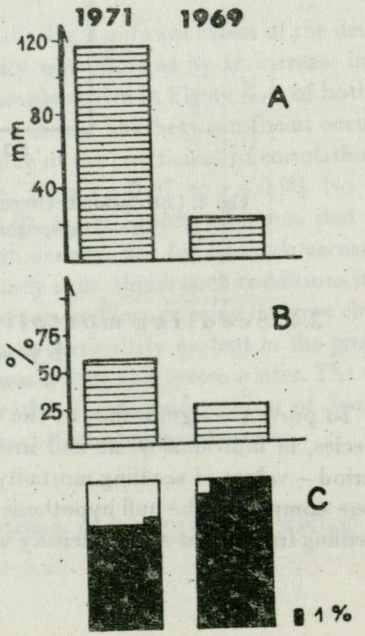

Fig. 6. Amount of precipitation (*A*) and percentage of days with precipitation (*B*) during the seedling phase, and the mortality of *Corynèphorus canescens* seedlings (*C*)
Black areas – per cent mortality relative to total number of seedlings in 1969 (right) and in 1971 (left)

Significant differences were found for the mortality of seedlings in *Cerastium semidecandrum* when data for 1968 and 1969 were compared; at similar densities they amounted on an average to 30%. At the same time in these years the greatest differences were recorded for minimum daily air temperatures during the period corresponding to the seedling phase of *C. semidecandrum* (Fig. 5).

Significant differences in the mortality of seedlings, only slightly smaller, were found for *Corynephorus canescens* when data of 1969 and 1971 were compared; the weather conditions that accompanied the seedling phase in these years differed considerably in respect of the quantity and frequency of precipitation (Fig. 6).

The mortality of seedlings of the rest of species in the years compared was very similar, and so was the rate of their mortality.

In all the species, especially in the populations of the perennial species, there occurred quite considerable differences between the individual years as regards the starting date of a seedling phase and its length. In extreme cases, in *Corynephorus canescens*, differences in germination dates amounted to one and a half months, and to as much as 5 months – in the phase length. This problem, however, is the object of the author's separate studies.

3.5. Sequence of appearance of the seedlings and their survival

Detailed observations have shown that in the majority of cases the most likely to survive were those seedlings which were the first to appear in a population. The mortality of this group of seedlings of all the species studied ranged only from 0 to 16%. Seedlings that appeared later survived in a much lower percentage, the survival decreasing rapidly with the time, down to zero.

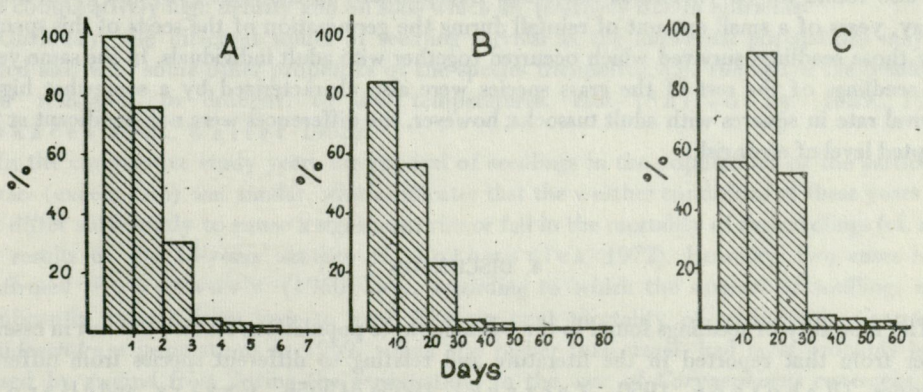

Fig. 7. Percentage of survivors relative to the percentage of seedlings sprouted during successive days or 10-day periods

A – Androsace septentrionalis, B – Tragopogon heterospermus, C – Corynephorus canescens

Examples of the relationship discussed have been illustrated in Figure 7 *A, B*. The only exception to this almost general rule was found in the case of *Corynephorus canescens* in 1969 (Fig. 7 *C*): for those seedlings that came up during the first 10-days' period of germination a

lower per cent survival was recorded than for those that came up during the second 10-days' period. This was probably caused by the drought, accompanied by a fairly high air temperature, comprising even a half of the second 10-days' period of the seedling phase.

It should be noted that in the calculations of the percentage of survived seedlings, depending on the sequence of their appearance, data from squares of low, medium, and high density were considered separately, and it has been found that the basic picture of the relationship between the sequence of appearance of the seedlings and their survival did not vary considerably with the varying density. Only in areas with the highest density of seedlings (especially in *Cerastium semidecandrum* and *Corynephorus canescens*) merely those individuals which had appeared first survived, whereas all the others died.

3.6. Effect of adult individuals on seedling survival in populations of polycyclic species

The comparison of seedling mortality between areas occupied only by seedlings, and areas in which in addition to seedlings there were also adult individuals was carried out – separately for several seedling density classes (with a varying number of classes and a varying number of individuals in one class depending on species),and 3 density classes of adult individuals (1–2, 3–5 and 6–8 individuals per 0.25 m^2). In this case the approximate test of Cochran and Cox (Oktaba 1966) was used. A similar approach was used to check the differences in seedling mortality in the experimental plots.

The analysis did not reveal any statistically significant differences, thus no effect was found of adult individuals on the survival of seedlings in the populations of: *Koeleria glauca*, *Festuca duriuscula* and *Scleranthus perennis*. Except for two cases, a lack of significant correlation between the mortality of seedlings and the presence or absence of older generation individuals was also found for *Corynephorus canescens*. Exceptionally in the years 1969 and 1973, that is to say, years of a small amount of rainfall during the germination of the seeds of this species, only those seedlings survived which occurred together with adult individuals. In the same years the seedlings of the rest of the grass species were also characterized by a somewhat higher survival rate in squares with adult tussocks; however, the differences were not significant at the adopted level of error risk.

4. DISCUSSION

The mortality of seedlings found in the psammophyte populations studied did not in essence differ from that reported in the literature and relating to different species from different biotopes (Rabotnov 1950, Zarzycki 1965a, 1965b, Cavers and Harper 1967a, Mathews and Westlake 1969 and others). It was relatively high in all populations and varied little from year to year.

The magnitude of seedling mortality showed no relationship to the number of seedlings appearing in the populations, which can be exemplified by the following two cases: (1) the mortality rates in *Corynephorus canescens* and *Koeleria glauca* populations were very high and nearly identical, the number of seedlings of the former being every year 200 up to 500 per square metre, and of the latter 65 at the most; (2) the lowest, of all those found, per cent

mortality of *Cerastium semidecandrum* and *Androsace septentrionalis* seedlings; these two species always differed in the number of seedlings per 1 m^2 by 500–550 (there were more seedlings in *C. semidecandrum* populations).

However, the results indicate a clear relationship between the mortality of seedlings and length of the life cycle and the type of reproduction of the particular species. The increase of the mortality rate, from the annuals (especially from the ephemers which live the shortest) to the perennials (with a maximum for vegetatively propagating species), agrees with the direction described by Rabotnov (1950), and confirms the different reproductive strategy and tactics of mono- and polycyclic plants (Harper and Ogden 1970). In the case of annual species the survival of seedlings is much more important for the continuation of the species than in the case of perennial species which live for many years and are capable of producing offspring every year.

To confirm the concept of Harper and Ogden (1970), there was almost a complete mortality of the seedlings of *Koeleria glauca* and *Festuca duriuscula* which propagated mainly vegetatively. A similarly high mortality of the seedlings of perennial species with a vegetative type of reproduction was observed by Tamm (1956), Rabotnov (1960), Putwain, Machin and Harper (1968) and Putwain and Harper (1970).

The results obtained also permit the statement that the mono-, bi- and polycyclicity of a population, which is a character of the species, plays a more important role in the survival of seedlings than do the habitat conditions, different or identical. An example to prove this is the fairly great difference in the mortality of seedlings between a one-year population of *Spergula vernalis* and a perennial population of *Corynephorus canescens* which occupied in the study area (as they usually do in Poland) identical habitats, and were characterized by a similar, high production of seedlings. Other proof was provided by the small differences in the mortality of the seedlings of the perennial grasses: *Corynephorus canescens* and *Festuca duriuscula*, which occupied – as a result of the diversity of dune habitats – different micro-habitats: the former occurring on bare, winnowed, almost humus-less sands, and the latter in patches of vegetation of a comparatively high density and on soils which are relatively rich in nutrients.

Obviously, the different values of seedling survival in the individual populations may be linked also with some other properties of the species themselves, e.g., the size of the seedlings, their resistance to drought, to low temperatures, etc. (Salisbury 1929, 1942, Sukačev 1953, Walter 1962).

In the consecutive study years the survival of seedlings in the populations of the particular species (except two) was similar, which indicates that the weather conditions of these years did not differ sufficiently to cause a significant rise or fall in the mortality of the seedlings (cf. also the results of the 14-years' studies of Antonovics 1972). However, two cases have confirmed Rabotnov's (1960) view, according to which the survival of seedlings may significantly change from year to year. The per cent mortality of seedlings in *Cerastium semidecandrum* populations in 1969, which was higher than usual, had most probably been caused by ground frost during the germination. In the case of *Corynephorus canescens* the lowered survival of the seedlings in the same year, as compared with other years, resulted most likely from the drought, to which the seedlings of this species (as well as the adult individuals) show a low resistance, especially when compared with *Koeleria glauca* which occurs in similarly dry habitats (Rychnovská-Soudková 1961, Rychnovská 1963, Rychnovská and Květ 1963, Marshall 1965, 1967).

The rate of seedling mortality in the populations of the species studied was not even during the seedling phase. Considered in absolute time units, the highest mortality rate occurred in

those species which live the shortest. However, during the successive periods of the seedling phase, these varying in length from species to species and from year to year depending on the phase length, a considerable similarity could be seen in the course of seedling mortality. The percentage of dying (and appearing) seedlings was always the highest in the first period and it clearly decreased thereafter. This was most likely connected with both the highest initial density of seedlings and their high susceptibility during the earliest stage of their life (Rabotnov 1950). It should be noted here that most of the seedlings which died in the later periods were seedlings which were also the latest to appear in the population. This regularity was seen in all the species studied.

In most cases the mortality of seedlings clearly decreased with time. An exception was a growth of mortality in the last period of the seedling phase of three species: *C. canescens*, *S. vernalis* and *T. heterospermus*. In the former two populations the increase in mortality may have resulted from the adverse effect of the weather conditions in winter. As regards *T. heterospermus* – the cause was different, most likely the competitive action of the fast growing last-year's individuals which overgrew the seedlings. This was indicated by the fast that it was in the immediate neighbourhood of the second-year individuals that most of the dead seedlings found during that time had died.

A statistically significant, negative effect of the density of seedlings on their survival was seen in most species. The growth of mortality rates with increasing densities was the object of many studies carried out both in natural populations and in cultures (Marschall and Jain 1969, Mathews and Westlake 1969, White and Harper 1970, Symonides 1974b, Wilkoń-Michalska 1976). According to the opinion held by Ross and Harper (1972), after the appearance of the seedlings their survival, further development and growth rate are most affected by the density. This is no doubt connected with the competitive struggle among individuals of the same generation occupying a similar ecological niche (McNaughton and Wolf 1970, and Gause 1934 quoted therein). This competition is particularly strong in the root zone of the plants (Sukačev 1953, Karpov 1962, Caplenore 1964, Zarzycki 1965a, 1965b, Litav and Wolovitch 1971).

The exceptional survival of a greater percentage of the seedlings of *Spergula vernalis* in areas of a higher density in 1971 confirmed the principle put forward by Alle (Alle et al. 1958) that unfavourable to a population may be not only a very high level of density, but also a very low level of density. In the case described, the advantages of the remaining seedlings in a group during the severe winter were greater than the losses caused by the limitation of space.

When considering the effect of density on the survival of seedlings, it should be noted that the maximum density of seedlings at the time when they passed on to the next developmental stage varied considerably from species to species, in extreme cases amounting – as adjusted to the per 1 m^2 basis – about 16 thousand individuals of this generation (*Cerastium semidecandrum*). This is certainly connected with the different types of growth of the species studied, thus with smaller or larger individual areas (Aulak 1976); rosette (*Androsace septentrionalis*), or tussocky (grasses) seedlings naturally require more space than do the minute seedlings of *Cerastium semidecandrum*.

Related to the problem of individual areas is another matter: the effect of an earlier or later appearance of seedlings on their survival. Those seedlings which appeared sufficiently early – the first seedlings of the population – survive in a much larger proportion, as compared with those which appeared later. This is most likely connected with the fact that the first seedlings have the possibility to occupy a larger living space (Ross and Harper 1972).

This is particularly important as far as the space underneath the soil surface is concerned, for according to the results published by Cavers and Harper (1967b) and by Harris and Wilson (1970), a fast root growth and the root competition play an important role in the survival of seedlings. In the case of the rosette-shaped seedlings of *Androsace septentrionalis*, important also is the space on the soil surface. The observations indicated that each later sprout appearing under the rosette of a seedling that had come up earlier died within a very short time.

In general, the studies did not reveal any relationship between the presence or absence of adult individuals in a polycyclic population and the survival of seedlings. The low density of adult individuals in the dune communities, and the ecological niches, which they occupy and which differ from those occupied by the seedlings, did not cause a sufficiently strong "competitive pressure" (Zarzycki 1965a, 1965b) to lower the survival of seedlings. Moreover, for all grass species a slightly higher rate of seedling survival in the years of droughts was found in the neighbourhood of adult individuals. In the case of *Koeleria glauca* and *Festuca duriuscula*, those seedlings, which were deeply rooted in the rhizosphere of large tussocks, had a better water supply than the remaining seedlings. These species have the ability to store water in the root zone for a later use during periods of drought (Rychnovská-Soudková 1961, Wilkoń-Michalska and Symonides 1974). *Corynephorus canescens* does not possess this ability, and in the spring and in summer it tends to dry the soil within the reach of its roots. This is surely connected with the intensive transpiration characteristic of this species (Rychnovská-Soudková 1961). In this case, however, adult tussocks protect seedlings against being buried by drift sand, as well as against the exposure of their roots. This phonomenon could be observed fairly often during spells of dry and windy weather.

The present studies did not provide much information on the effect of the competition between the seedlings of different species present in the same common area. The germination dates of the different species whose seedlings grew together were either different or coinciding only to a small extent. Although the seedlings of *Spergula vernalis* and *Corynephorus canescens*, occurring in the same patches, appeared at very similar dates, they usually formed spatially separate, larger or smaller, one-species clumps. For the same reason it was not possible to find the negative effect, known from the literature (Zarzycki 1965b), of adult individuals of one species on seedlings belonging to another species.

5. CONCLUSIONS AND FINAL REMARKS

The results obtained from the studies permit the following conclusions to be made:

1. the relatively high seedling mortality, varying little from year to year, depended primarily on the length of the life cycle and the type of reproduction of the individual species;

2. the lowest seedling mortality was recorded for the populations of annual species and the highest – for populations of perennial species, especially those capable of vegetative propagation;

3. the seedling mortality course of the different species was found to be similar: the largest percentage of seedlings always died (and appeared) in the early period of the seedling phase, whereafter it gradually decreased;

4. the largest percentage of survivors consisted of seedlings that had appeared during the early period of germination; seedlings that had appeared in a later period died in much larger numbers;

5. in most cases there was a close relationship between the density of the seedlings and their survival: an increase in density caused a growth in seedling mortality.

During the investigations, as also after a detailed analysis of the results, a number of problems emerged related directly or indirectly with the problem of seedling survival which, according to the author, deserve attention. The following questions arose: (1) why do seedlings of one species appear in larger numbers than those of another species in spite of the fact that their seed production and habitats are similar? (2) what are the factors which cause the differences in the dates of appearance of seedlings, due to which the individuals that appeared earlier have a much greater chance to survive? (3) what are the causes of the mosaic structure of the vegetation on sands, thus why do seedlings usually grow in large clumps, leaving quite free space close by?

Not all the questions can be answered on the basis of studies of natural populations. Certain problems require experiments to be carried out which would in conjunction with investigations under natural conditions make it possible to better understand the complex mechanisms controlling the process of seedling mortality.

6. SUMMARY

The paper presents some of the results of the author's 7-years' studies concerned with the mortality of seedlings in natural populations of the following species: (1) *Cerastium semidecandrum*, (2) *Androsace septentrionalis*, (3) Plantago indica, (4) *Trifolium arvense*, (5) *Spergula vernalis* (annuals), (6) *Jasione montana*, (7) *Tragopogon heterospermus* (biennials), (8) *Corynephorus canescens*, (9) *Festuca duriuscula*, (10) *Koeleria glauca*, (11) *Scleranthus perennis* (perennials). The studies were carried out in the Basin of Toruń in the years 1968–1974 (Symonides 1974a).

The aim of the study was to determine the magnitude and the rate of seedling mortality in populations of species differing by their biology, living under similar habitat and climatic conditions, and to demonstrate the relationship between seedling mortality and their density, sequence of appearance, presence or absence of adult individuals, and weather conditions during the seedling phase.

On the basis of the studies the following have been found:

1. A relatively high, because exceeding 50% of the total number, mortality of the populations of all the species studied. The highest survival of seedlings was recorded for populations of annual species and the lowest – for populations of perennials, especially of those capable of vegetative reproduction (Fig. 1). The results agree with the data reported by Rabotnov (1950), and they confirm the concept, suggested by Harper and Ogden (1970), of a different reproductive "strategy" and "tactics" of annual, biennial and perennial plants.

2. A considerable similarity of the rate of seedling mortality in the early period of the seedling phase in spite of the existence of considerable differences in the total length of the phase (cf. Figs. 2, 3), and a great time coincidence of: the mass appearance of seedlings and their dying in large numbers (Fig. 3 *a*, *c*, *e*).

3. A close correlation between the density of seedlings and their mortality (Fig. 4 *A*); this correlation was not found in the populations of species whose seedlings did not form very dense clumps (Fig. 4 *B*). The correlation between the density and mortality of seedlings has confirmed the results of the studies carried out by Marschall and Jain (1969), Mathews and Westlake (1969), White and Harper (1970), Wilkoń-Michalska (1976) and many others.

4. A close relationship between the per cent survival of seedlings and their earlier or later appearance in a population (Fig. 7 *A*, *B*); except for one case, mainly those seedlings survived which had been the first to occupy the living space, driving out, through competition, most of the seedlings that appeared later (Ross and Harper 1972).

The present studies have not revealed any significant effect of the presence of adult individuals on the survival of seedlings. The reason probably was that the level of density of the dune vegetation was low, and – therefore – there was not a sufficiently strong "competitive pressure" among the individuals of a diverse generation (Zarzycki 1965a, 1965b). Apart from two exceptions (Figs. 5, 6), there occurred no close relationship between the mortality of seedlings and the varying weather conditions of the particular study years.

7. POLISH SUMMARY (STRESZCZENIE)

W pracy przedstawione są niektóre wyniki 7-letnich badań poświęconych wymieraniu siewek w naturalnych populacjach następujących gatunków: 1) *Cerastium semidecandrum*, 2) *Androsace septentrionalis*, 3) *Plantago indica*, 4) *Trifolium arvense*, 5) *Spergula vernalis* (jednoroczne), 6) *Jasione montana*, 7) *Tragopogen heterospermus* (dwuletnie), 8) *Corynephorus canescens*, 9) *Festuca duriuscula*, 10) *Koeleria glauca*, 11) *Scleranthus perennis* (wieloletnie). Badania przeprowadzono w latach 1968–1974 w Kotlinie Toruńskiej (Symonides 1974a).

Celem pracy było określenie rozmiaru i tempa wymierania siewek w populacjach gatunków o odmiennej biologii, w podobnych warunkach siedliskowych i klimatycznych oraz wykazanie związku między śmiertelnością siewek a ich zagęszczeniem, terminem wyrastania, obecnością lub brakiem osobników dorosłych oraz warunkami pogodowymi towarzyszącymi fazie siewki.

W wyniku przeprowadzonych badań stwierdzono:

1. Stosunkowo wysoką, bo przekraczającą 50% ogólnej liczby, śmiertelność populacji wszystkich badanych gatunków. Największe przeżywanie siewek charakteryzuje populacje gatunków jednorocznych, najmniejsze zaś – populacje gatunków wieloletnich, zwłaszcza tych, które mogą się pomnażać wegetatywnie (fig. 1). Wyniki te są zgodne z danymi Rabotnova (1950) i potwierdzają koncepcję Harpera i Ogdena (1970) o odmiennej „strategii" i „taktyce" reprodukcyjnej roślin jedno-, dwu- i wieloletnich.

2. Duże podobieństwo w intensywności wymierania siewek we wczesnym okresie fazy siewki, mimo znacznych różnic w całkowitej długości fazy (por. fig. 2, 3), oraz dużą zbieżność w czasie: masowego pojawiania się siewek i masowego ich wymierania (fig. 3 *a, c, e*).

3. Ścisłą korelację między zagęszczeniem siewek a ich wymieraniem (fig. 4 *A*); zależności tej nie stwierdzono jedynie w populacjach tych gatunków, których siewki nie tworzyły silnie zagęszczonych skupień (fig. 4 *B*). Zjawisko współzależności zagęszczenia i śmiertelności siewek potwierdziło wyniki badań Marschalla i Jaina (1969), Mathewsa i Westlake (1969), White i Harpera (1970), Wilkoń-Michalskiej (1976) i wielu innych.

4. Ścisłą zależność między procentem przeżywających siewek a wcześniejszym lub późniejszym ich pojawieniem się w populacji (fig. 7 *A, B*); poza jednym wyjątkiem przeżywają przede wszystkim siewki, które – jako pierwsze – zajmują przestrzeń życiową, wypierając w procesie konkurencji siewki wyrastające później (Ross i Harper 1972).

Badania nie wykazały istotnego wpływu obecności osobników dorosłych na przeżywanie siewek, prawdopodobnie wskutek słabego zwarcia roślinności wydmowej i – w związku z tym – niedostatecznie dużego „napięcia konkurencyjnego" między osobnikami różnej generacji (Zarzycki 1965a, 1965b). Poza dwoma wyjątkami (fig. 5, 6) nie wystąpiła także ścisła zależność między śmiertelnością siewek a odmiennymi warunkami pogodowymi w poszczególnych latach badań.

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