Ewa SYMONIDES

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

THE STRUCTURE AND POPULATION DYNAMICS OF PSAMMOPHYTES ON INLAND DUNES

IV. POPULATION PHENOMENA AS A PHYTOCENOSE-FORMING FACTOR (A SUMMING-UP DISCUSSION)

ABSTRACT: The results are discussed of studies dealing with (1) changes in psammophyte vegetation in the course of inland dune overgrowing, and (2) population characteristics of selected plant species, and their response to the phytocenotic and biotope conditions in the habitat (S y m o n i d e s 1979a, 1979b, 1979c). The studies have shown that the formation and succession of communities result from a complex but not chaotic interplay of environmental, population and biocenotic factors. Used for studies of the succession of phytocenoses, the population analysis method makes it possible to get an insight into the nature of the phytocenotic systems, and into the mechanisms determining the structure and dynamics of vegetation.

KEY WORDS: Inland dunes, psammophytes, populations of initial stages and of compact communities, environmental modifications of reproduction, effectiveness of generative and vegetative reproduction, survivorship curves, life strategy of monocarpic and polycarpic plants, density--dependent plasticity.

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*Correspondence address: Akermańska 5 m. 37, 02—760 Warsaw, Poland.

1. INTRODUCTION

All previous studies of psammophyte communities in Poland were mainly restricted to the analysis of the vegetation: description and classification of communities, and partially also their distribution and geographical differentiation. There are practically no data on the successions of inland psammophyte sods, and especially their inner dynamics, although each phytosociological paper takes into account — at least incidentally — developmental tendencies of the vegetation, both natural and those formed under the influence of man (cf. N o w i ń s k i 1967, K o r n a ś 1972, G ł o w a c k i 1975, and the literature quoted there). The lack of studies conducted regularly at permanent observation sites in similar, or different psammophyte communities makes it impossible to compare the results presented in the previous parts of this series (S y m o n i d e s 1979a, 1979b, 1979c), and especially the quantitative aspect of vegetation changes, with the results from the investigations carried out by other authors.

2. FORMATION AND GROWTH OF PSAMMOPHYTE COMMUNITIES

As has been revealed by studies, there is only a small number of psammophyte species which are capable of colonizing extremely unfavourable habitats. Dry, moving sands, which get strongly heated make impossible, or to a large extent limit the germination of seeds, and the growth and development of seedlings (M c W i l l i a m and P h i l l i p s 1971, A y y a d 1973, S h a r m a 1973, 1976, B h a n d r i and S e n 1975). Although in the surface layers of the sands there is a large number of diaspores accumulated, representing several dozen plant species (S y m o n i d e s 1978a), the initial community for many years consists only of two species (*Corynephorus canescens* (L.) P. B. and *Spergula vernalis* Willd.), whereas changes in the vegetation are only of a quantitative nature. Only after a certain threshold level of numbers has been attained by the populations of the pioneer components of the community (especially *C. canescens*) will there take place a basic change in the quality of the biotope, as manifested by a rapid enrichment in its species composition. The selection of species is characteristically being accomplished from the very beginning of the initial communities; thus from the beginning of the early phase of dune overgrowing the vegetation has a definite ecological nature and constitutes the initial developmental stage of a strictly specified association (S y m o n i d e s 1979a).

The dune overgrowing process is initiated by the settling of the first tussocks of *C. canescens*. In the immediate vicinity of the pioneer tussocks there appear, every year, more and more new individuals of the initial components of the community. Under the protection of *C. canescens* there also grow the first seedlings of most of the remainder of species — the components of Spergulo Corynephoretum (Tx. 1928) Libb. 1933, in somewhat later phases of

the development of the community. Thus the number and distribution of the pioneer individuals of *C. canescens* to a large extent determine the rate and course of the further overgrowing of sands.

As a consequence of the highly aggregated spatial population structure of the pioneer dune communities, not only is the efficiency of sand fixing low, but also the transformation of the habitat is uneven. It seems that the spatial differentiation of moisture and nutrients in dunes (cf. W i l k o ń - M i c h a l s k a and S y m o n i d e s 1974) begins at the earliest stage of sand colonization, and represents the most important cause of the "mosaic" pattern of the psammophyte vegetation. On account of the specificity of action of the individual plant species on their immediate environment, one may also hazard the statement that the degree of biotope heterogeneity increases as the phytocenose becomes richer, more complex and more differentiated within itself (cf. H a r p e r 1977).

It is difficult with complete certainty to pinpoint the factors which condition the germination of the first diaspores and the survival of the first seedlings that initiate the formation of a *C. canescens* population, and the development of vegetation (and soil) in extremely dry dune habitats. However, certain data indicate that most important of all is the accumulation in a unit space of a sufficiently large number of diaspores capable to retain within this space enough moisture which is essential to the germination. With this assumption, the ecological situation of the diaspores located within the assemblage would be particularly advantageous for some reasons: (1) inside the assemblage the diaspores are least exposed to the adverse effects of the high temperature of the sands in a hot summer, (2) they have the possibility to most fully utilize the moisture retained by the "lump" of diaspores, (3) they are subject to the most intensive action of the germination stimulating substances secreted by diaspores (cf. L i n h a r t and P i c k e t t 1973). Under such conditions, the ecological effect of coexistence would already be seen at the stage of diaspores in the soil.

A sudden emergence of seedlings on dunes hitherto "bare" is probably preceded by a gradual, long-term process of accumulation of diaspores a considerable proportion of which, as has been demonstrated by investigations, are blown away together with the sand, and whose number, relative to areas already fixed by vegetation, is small (S y m o n i d e s 1978a). Thus it is not only plants capable of germinating on dry soils that can settle under such conditions, but also those which produce a large number of easily germinating and easily spreading diaspores, the diaspores have got to be endowed with the ability to remain viable in the soil for a long time.

As indicated by studies carried out so far, diaspore dissemination is a more or less continuous process, and usually comparatively slow (R i d l e y 1930, P o o l e and C a i r n s 1940, B a k k e r 1960, Y o c o m 1968, P i j l 1969 and others). It is the resultant of many variables which include both plant characteristics and diaspore disseminating agencies. In the light of these considerations the overproduction of diaspores, which is common especially among the plants of open communities (S a l i s b u r y 1942, 1952), cannot be regarded as a "prodigality" of nature, for only when their number is immense will a few individuals get the chance to germinate.

The extremely difficult conditions of germination existing in the dry, moving sand, provide the basic barrier for many psammophyte species which are less adapted to the living under extreme conditions than is *C. canescens* and *S. vernalis*. The most important of the many adaptations (in addition to the production of large numbers of diaspores capable of germinating) is the "phenology" of germination, and in the case of *C. canescens* also the short prereproductive period. Thus the domination phase of *C. canescens*, and the initial phase of the

pioneer community under extreme conditions last much longer than could be expected on account of the spatial proximity of the floristically richer and more compact communities.

In ecological systems only slightly more favourable the process of sand colonization and the rate of changes in the initial communities are much faster. A characteristic feature is that *Festuca psammophila* (Hackel) Krajina, and *Koeleria glauca* (Schkuhr) DC. are among the first species settling in the initial patches. From the beginning of the development of the Spergulo-Corynephoretum the direction is thus becoming outlined of the successional changes, as a result of which the next link is formed in the series of psammophyte communities: Festuco-Koelerietum glaucae Klika 1931.

During the invasion, the growth in numbers of *F. psammophila* and *K. glauca* populations is fairly slow, because it depends on the recruitment, from outside the patch, of a large number of diaspores whose germinating capacity — as has been shown by the studies — is low (S y m o n i d e s 1979b). The two species are also characterized by a longer, relative to *C. canescens*, juvenile period, and it is only after 4—5 years that they are able to produce generative and vegetative diaspores. The relatively long existence of the Spergulo- -Corynephoretum, and in any case the comparatively long dominance period of *C. canescens* seems to depend on the slow rate of the net increase of the populations of these species at the early stages of the invasion and their growth in numbers. As they grow in abundance, *C. canescens* — a competitively weaker species — is gradually displaced, whereas in very compact sod communities it does not find favourable conditions for reproduction (S y m o n i d e s 1979c).

F. psammophila and *K. glauca* are adapted to a wider range of differentiation of the psammophyte communities. Owing to their ability to produce both types of diaspore (vegetative and generative), a high viability of the offspring, longevity of individuals, and above all due to the ability to store water in the root zone — the two grass species belong to the dominating components of most psammophyte communities in the study area. It has also been found that their sensitivity to any disturbances in the phytocenose is low. Their root systems, which are extremely strongly developed and compact, to a large extent make it difficult for the seedlings of other species to settle in their vicinity. They were among the few species which survived the expansion of *Tragopogon heterospermus* Schweigg. (on site 6), and persisted for the longest time in the sod gradually occupied by *Carex arenaria* L. (S y m o n i d e s 1979b). *Festuca duriuscula* L., appeared to be competitively stronger. It gradually displaced first the *K. glauca* tussocks and then also those of *F. psammophila*; on completely fixed sands the sod is made up mainly of *F. duriuscula* (S y m o n i d e s 1979c).

It should be noted here that in the course of dune overgrowing the most important component of the communities is always the population of one of the above-named grass species. The remainder of the species covered by the research either dominate for a short time in the patch (*C. arenaria, T. heterospermus*) or — because of their small size and short life cycle — do not play any significant role in it, although their numbers are large (*Cerastium semidecandrum* L., *Androsace septentrionalis* L.), or they do not attain numerical predominance over the remaining species in any community, or are dominant only in some years (*Jasione montana* L., *Plantago indica* L.).

As the overgrowing of sands goes on it is primarily the perennial plant populations, propagating vegetatively, that have the chance to maintain or increase their numbers, this being most likely connected with a gradual deterioration of the conditions affecting the growth of the seedlings. Noteworthy is the fact that in the most compact patches the few populations that

reproduce only generatively belong to species with extremely short life cycles, restricted to the early spring period (*Androsace septentrionalis, Cerastium semidecandrum, Arenaria serpyllifolia* L.). In the case of this plants the short life cycle is the basic adjustment to the living in conditions of a strong competition from perennials, for it is only in the early spring period that the life activity is not yet marked of grasses dominating in very compact communities.

The existence of conditions unfavourable for the growth and development of seedlings in compact psammophyte communities also arouses doubts as to whether the succession of plants goes through compact sods to communities of the alliance Dicrano-Pinion, as commonly assumed (cf. N o w i ń s k i 1967). Observations have shown that pine seedlings emerge and survive only in loose sods of the association Spergulo-Corynephoretum, and occasionally also in the least compact patches of Festuco-Koelerietum glaucae; but they are never components of á highly compact vegetation. It seems that a pine-wood community can only replace compact sods when the pine invades the area at early stages of the development of psammophyte communities, or if a woodland community expands its biochore by a slow front invasion.

3. POPULATION CHARACTERISTICS OF PSAMMOPHYTES IN VARIOUS SYSTEMS OF PHYTOCENOTIC AND BIOTOPE CONDITIONS

3.1. POPULATION REPRODUCTION

3.1.1. General

Studies, conducted for several years, of the ecology of selected psammophyte species have revealed a causal interrelationship between the structure and functioning of a population, and all the biotopic and phytocenotic conditions of their living. During the overgrowing of the dune the basic population reaction to changes in these conditions was an increase, or decrease in numbers, or maintenance of a relative balance of numbers. In dune communities of a simple composition and structure the level of abundance of the population of a species at the same time determined its dynamic value and habitat-formative role, which was particularly marked in the early phases of the formation and growth of the initial communities.

Population abundance is to a large extent an exponent of the reproductive potential to which at least several elements contribute: (1) the "reproductive capacity" of the organisms, (2) the survival of the progeny until their reproductive maturity, (3) the fraction of progeny attaining reproductive maturity, and (4) fecundity during the reproductive stage (R i e g e r, M i c h a e l i s and G r e e n 1974). H a r p e r (1977) stresses also the important role of diaspore dissemination.

The estimation of the biotic potential of natural plant communities continues to be one of the most difficult tasks, and inherent in it is usually a considerable error. Controversial is the very criterion of a correct assessment of maximum reproductiveness, on the basis of which the reproductive potential of the population is estimated. According to O d u m (1977), a measure of the maximum reproductiveness of plants 'is the number of diaspores produced under optimum environmental conditions. Diaspore production is a certain exponent of the reproductive potential of the population (and, as has been shown earlier on, under extreme conditions it probably constitutes the basic factor conditioning the expansion of a population). However, the treatment of diaspores (and of seeds in particular) as propagation units equivalent

to the viviparous progeny (cf. F a l i ń s k a 1977) arouses doubts. It has been known for a long time that even under appropriate conditions not all the diaspores germinate, and there are plants which have almost entirely lost the ability to produce seeds capable of germinating (M u k e j r i 1936, F a l i ń s k a 1977). This is a phenomenon particularly frequent among plants which at the same time produce vegetative diaspores (Z a r z y c k i 1964, P e r m a d a s a and L o v e l l 1974, F a l i ń s k a 1977, S y m o n i d e s 1978a).

The germinating capacity of the diaspores of the species under study was from 1.1% in *J. montana* to 86.7% in *T. heterospermus;* however, in none of the populations did it attain 100%. Moreover, sowing diaspores in experimental plots has proved that under natural conditions the germinating fraction is even smaller than in the laboratory. It seems, therefore, that the value of the biotic potential, or of the maximum reproductiveness of a population, as calculated from diaspore production, is almost an abstraction, since the low germinating capacity, the environmental resistance, or entirely chance factors rule out the possibility to realize this "potential".

Not fewer are the objections aroused by the possibility to indicate the "optimum" environmental conditions under which the fullest possible realization of the reproductive potential of a population would take place. The probability of a set of abiotic and biotic factors, the best ones for a particular population, occurring over a period of several, and even of between ten and twenty years, is no doubt very low. The creation of such "optimum" conditions in culture is more probable, but the reproductive potential of a cultured population should not be used as a point of reference in the interpretation of the reproductiveness under natural conditions, for in accordance with the more recent views the biotic potential is the character of a population and not of a species.

Depending on what is considered to be the "progeny", diaspores, or seedlings should constitute the initial population in studies of its survival. There is no doubt that under natural conditions, at least on account of the uneven germination of seeds, which is sometimes spread over several years, it is the number of seedlings that can provide the starting point in the estimation of the survival of a population. The total number of diaspores is more and more often used as a measure of reproductiveness, and is treated as a reference system in the estimation of population mortality only under laboratory conditions (P a l m b l a d 1968, S h a r i t z and M c C o r m i c k 1972), whereas only the number of emerged seedlings is considered to be a better criterion for natural populations (S a r u k h á n and H a r p e r 1973, M a c k 1976, M a c k and H a r p e r 1977); in the latter case, the production of dias-pores is estimated independently and can be treated as an approximate measure of the potential fecundity of the population.

In the discussion on what should be considered the real progeny of a plant, and thereby the measure of reproductiveness, most convincing seems to be the attitude of H a r p e r and W h i t e (1974) who are of the opinion that equivalent to births is the germination of plant seeds, because it is only then that "the embryo escapes from maternal investing tissues and acquires independence". In the previous papers of this series and further in this discussion "progeny" refers to seedlings or rooted vegetative propagules (cf. S y m o n i d e s 1979a, 1979b, 1979c).

3.1.2. Environmental modifications of reproduction

A comparison of the reproductiveness of the psammophyte species studied shows that the reproductive capacity is to a large extent the function of the mode of reproduction: with the

generative reproduction the numbers of the progeny per one parent individual were usually higher than in the case of production of both types of diaspores, or only vegetative propagation. Furthermore, it has been found that in the populations of species producing both types of diaspores the manner of reproduction is subject to strong environmental modifications, while the ratio of the number of generative offspring to that of the vegetative one changes with the age of the population (cf. also Z a u g o l n o v a 1972, F a l i ń s k a 1976). A general regularity was the generative reproduction or its considerable predominance during the colonization of new areas and in early periods of population growth, and its complete disappearance, or a considerable limitation with increasing population density, a general increase in the density of the vegetation in the patch, and a stabilization of the phytocenotic systems (S y m o n i d e s 1979a, 1979b, 1979c).

In some species the transition from generative to vegetative reproduction is gradual, e.g., in *Koeleria glauca*, *Festuca psammophila*, *F. duriuscula*, while in others – generative reproduction is manifasted by a single "big-bang" (cf. H a r p e r and W h i t e 1971), whereas later growth in numbers is accomplished exclusively, or almost exclusively, by vegetative propagation. It is possible to include in the second group not only *C. arenaria*, but also several other species which, having initially colonized the new area, for the subsequent eight years did not produce any seedlings, but multiplied only vegetatively, e.g., *Helichrysum arenarium* (L.) Moench, *Hieracium pilosella* L., *Thymus serpyllum* L., and many others.

These investigations have shown that regardless of the changed way of reproduction, populations of the same species produced similar numbers of generative diaspores, and what is more – with a similar germinating capacity. Thus the transition from generative to vegetative reproduction did not result from a reduction in the potential possibilities of a plant to reproduce generatively, nor did it cause a reduction in the production of viable diaspores. This was most likely a manifestation of the adaptation of the population to the deteriorating conditions which affected the growth of seedlings as the sands became overgrown by a more compact vegetation.

The yearly production of viable seeds in populations reproducing only vegetatively may be considered as evidence of an "irregular overproduction", particularly because some species (e.g., *C. arenaria*) utilize for their production as much as 50% of the biomass produced (S y m o n i d e s 1979b). From the viewpoint of population energetics, this is a phenomenon difficult to explain, but it indicates a strong genetic background; consequently, the developmental cycle of the plants, and to broadly understood "reproduction strategy" are realized independently of the way of reproduction to which the population has become adapted, and which is possible under the particular ecological conditions (cf. F a l i ń s k a 1977).

3.1.3. Effectiveness of vegetative and generative reproduction

The vegetative reproduction was low in all the psammophyte species studied, and it varied slightly from year to year. The rate of multiplication depended not only on the age of the parent individuals, but to a large extent also on the presence of a free space in the immediate surroundings. In very compact sods, new individuals of *K. glauca*, *F. psammophila* and *F. duriuscula* emerged only after the death of the old tussocks in the places occupied by the latter (S y m o n i d e s 1979c).

The large number of generative diaspores in species reproducing exclusively by seeds can be considered in terms of "irregular overproduction". The abundance of diaspores produced and

the disproportionately small number of seedlings indicate poor possibilities to realize their potential. It should be emphasized that in general the reproductiveness of the psammophytes is not directly related to the number of diaspores produced. Such a relationship exists only at the earliest stages of life of the pioneer populations, with the phytocenose "lacking fullness" in respect of the individuals of the particular components (R a b o t n o v 1960a, S y m o n i d e s 1974, W i l k o ń - M i c h a l s k a 1976). Diaspore "over-production" is conspicuous at a comparatively early stage, and it grows continuously in progressive populations, along with the growth of the number of individuals able to reproduce. It may also be assumed that with the gradual stabilization of the system, the ratio of total diaspore production and the fraction of germinating diaspores remain at more or less the same level (e.g., in *C. canescens* at site 3, in *C. semidecandrum* at sites 9, 10).

3.2. THE LIFE OF A POPULATION AT THE STAGE OF DIASPORES IN THE SOIL

Beneath the soil surface there accumulates a large number of seeds which fail to germinate. Fixed dune sands contain an impressive seed "bank". In surface-layer sand samples, taken only sporadically in different patches of Festuco-Koelerietum glaucae, 38—48 thousand diaspores per $1 m^2$ of soil were found (E. Symonides — unpublished data). For comparison — B r e n c h l e y and W a r i n g t o n (1930, 1945) report 39 to 75 thous. for crop fields, R a b o t n o v (1956a) and G o l u b e v a (1962) found in various meadow soils from several to over twenty thousand, Z a r z y c k i (1964) found in the Carpathian beechwood from 1700 up to 2200 diaspores; on the poorly overgrown dune sands of the Toruń Basin 1900—3500 diaspores were found (S y m o n i d e s 1978a).

The fate of the diaspores shed on the surface of the soil is relatively little known. In an open space a certain number of them are carried out of the community boundaries; on the other hand, diaspores sometimes remain in the ·soil for many years, hence their species composition only to a small extent represents the species composition of the vegetation on the surface of the ground (M a j o r and P y o t t 1966, S y m o n i d e s 1978a). Some of the diaspores penetrate, together with the rain-water, into deeper soil layers whereby they practically lose the opportunity to germinate. In soils with a rich fauna some of the diaspores are eaten (R a b o t n o v 1954, 1960a). Nevertheless, in various plant communities, beneath the soil surface there is always a large accumulation of seeds able to germinate.

From the few studies hitherto carried out follows that only 1—4% of the diaspores develop into seedlings (K r o p a č 1966, Barallis 1968 after H a r p e r 1977, N a y l o r 1972a, 1972b). The remainder of them die, or for many years retain the ability to germinate, depending on the biological characteristics of the plants and the properties of the soils (K n a p p 1954, N o w i ń s k i 1967, R o b e r t s 1972, R o b e r t s and F e a s t 1973), the vegetative propagules being less durable than the seeds (R a b o t n o v 1950).

Certain data indicate that the seeds of annuals remain viable for a longer time than those of the perennials (C h a p n e s s and M o r r i s 1948, M a j o r and P y o t t 1966, W e n t 1973). Different results have been reported by P e r m a d a s a and L o v e l l (1974): the diaspores of dune annuals germinate only during one growing season whereafter almost all of them die. On the other hand, R a b o t n o v' s (1956a) studies indicate that the germination of meadow perennials is spread over many years. Thus the data quoted above, and many others, show that a population of viable diaspores in the soil possesses its own "life strategy", which

often differs from the strategy of the plants that produce them (H a r p e r and W h i t e 1971, R o b e r t s 1972. R o b e r t s and F e a s t 1973). This represents yet another argument showing that the status of the diaspore as a full-value individual of a population is doubtful.

3.3. DIASPORE GERMINATION

Whether or not a seed potentially capable of producing a seedling will germinate is to a large extent a matter of chance, and depends on whether the seed finds itself in a "safe place" (H a r p e r, W i l l i a m s and S a g a r 1965). Moreover. experimental investigations into the germination and survival of psammophyte seedlings have proved that very important is also the depth at which the seeds are. It has also been found that a higher percentage of seedlings emerge from large seeds sown at a relatively low density (S y m o n i d e s 1978b). The above-indicated relationships are directly connected with the growth of the germs, and not with the germination of the seeds. The advantages of a shallow sowing, higher contents of reserve substances in the seeds. and of a low density of the latter, when the biotope is poor in nutrients, have been known from many studies, and have many times been discussed in the relevant literature (B l a c k 1956, 1963, G r i m e and J e f f r e y 1965, T w a m l e y 1967, R o s s and H a r p e r 1972, S y m o n i d e s 1978b, and others). For this reason, diaspore "over-production" by plants of extreme habitats becomes understandable, since a high diaspore density on the one hand conditions the germination, and on the other hand most of the seedlings that appear in a very compact growth are doomed to death. All these data also indicate that the number of really germinated seeds in the soil is much higher than could be estimated on the basis of the number of seedlings, and a considerable percentage of the germs die before they are able to emerge above the soil surface as seedlings. This would at the same time indicate that the number of seedlings is also an approximate measure of the fecundity of a population.

Relatively little is known about the effect of adult individuals of a population on the further fate of the diaspores. It has been known, however, that it is not entirely favourable nor entirely adverse. The above-ground parts of adult plants retain a certain number of diaspores thus making it impossible for them to get into the soil (W i l k o ń. – M i c h a l s k a 1976), while on the other hand under certain conditions in open spaces they prevent them from being blown away (S y m o n i d e s 1974, 1978a). The effect of adult plants on the microhabitat and microclimate may also bring advantages for the diaspores (by reducing the large amplitude of daily temperatures in the surface layers of the sands), or be adverse (because of the toxic root secretions, soil overdrying, etc.). Connected with the latter effect is probably the failure to germinate of the nutlets of *C. arenaria*, caryopses of *C. canescens* and of others within a sedge sod.

3.4. THE SURVIVAL AND DEATH OF SEEDLINGS

A comparison of the reproductiveness of the populations of the different species studied, and of different populations of the same species shows that the progeny production "capacity" is the resultant of many factors, being to the same extent determined by the biological properties of the plants as by the environment in the broad sense. Among the environmental

factors, except those of the extreme habitats, the space available to the seedlings, or vegetative progeny, plays an important role (cf. H o l t 1972), and so does the number of "safe places for the germination of seeds" within a biochore (H a r p e r, W i l l i a m s and S a g a r 1965).

The density of seedlings attained by the populations of the psammophytes studied only to a small extent reflects their real fecundity, and the differences between the total number of seedlings emerged and their maximum density in the same unit area depend on the length of the germination period, the longer the period, the greater the differences. This is connected with the early mortality of seedlings. In the populations of the species studied, except *Cerastium semidecandrum* and *Androsace septentrionalis*, half of the total number of seedlings die before the germination of the last seeds (S y m o n i d e s 1979b). Thus the competition among individuals occupying the same ecological niche is visible from the beginning of their life (M c N a u g h t o n and W o l f 1970).

The total mortality of seedlings was in each population relatively high and, except *Plantago indica*, it varied little with the years; in this respect the psammophytes do not differ significantly from the plants of other ecosystems (R a b o t n o v 1950, C a v e r s and H a r p e r 1966, M a t h e w s and W e s t l a k e 1969, H a w t h o r n and C a v e r s 1976, W i l k o ń - M i c h a l s k a 1976). Clearly noticeable is also the relationship between the mortality of the seedlings and the duration of the life cycle and type of reproduction of the particular species. The fact that the death rate is relatively low in the populations of annuals, but very high in the perennials capable of repeated production of seeds (and seedlings) during ontogenesis (especially in the populations of species at the same time multiplying vegetatively) shows that the reproductive "strategy" and "tactics" of the mono- and polycyclic plants are different, which has been many times signalled in various ecological papers (T a m m 1948, 1956, 1972, R a b o t n o v, 1956b, P u t w a i n, M a c h i n and H a r p e r 1968, H a r p e r and O g d e n 1970, P u t w a i n and H a r p e r 1970, S y m o n i d e s 1974, 1977, M a c k 1976, M a c k and H a r p e r 1977).

The causes of the mass mortality of seedlings are not yet well known, although the investigations carried out so far indicate that the most important factor limiting their number is overcrowding. It causes a strong "competitive pressure" among the individuals of the same age whose space and food requirements are similar (Z a r z y c k i 1965, H a r k e s s 1970).

The relationship between the number of seedlings per unit area and their survival was the object of laboratory and field studies (Y o d a et al. 1963, M a r s c h a l l and J a i n 1969, M a t h e w s and W e s t l a k e 1969, R o s s and H a r p e r 1972, S y m o n i d e s 1977). From these studies follows that seedling density not only exerts the most important influence on the survival of the seedlings, but it also affects the growth rate and the further development of the plants. It is only under extremely adverse living conditions that the chance to survive of young individuals in larger aggregations is greater than that of those growing singly, or at low densities: when exposed to being buried in moving sand, seedlings of *Corynephorus canescens* and of *Spergula vernalis* (site 1) survived in much larger numbers if they formed more compact aggregations (S y m o n i d e s 1974, 1979a).

An increased density also increased the chance to survive for the seedlings of *Androsace septentrionalis* exposed to the competitive action of the seedlings of *Tragopogon heterospermus* — a competitively stronger species; a situation like this occurred when a long period of ground frost caused a delay in the coming-up of the seedlings of *A. septentrionalis*. In two-species systems the effect of density on the survival of the seedlings in a population sometimes depends on the competitive power of the partner (H a r p e r and C h a n c e l l o r

1959, Z a r z y c k i 1965 and the references therein quoted). If the competitive power is the same — as in the case of *Plantago indica* and *Salsola kali* L. — the seedlings of each population react in the same way to an increased density of the individuals of their own population as to that of the partner (cf. H a r p e r and W h i t e 1971). In general, the studies have shown, however, that the density-dependent mortality is peculiar to species, and even to a particular population of the same species (cf. also H a r p e r and M c N a u g h t o n 1962).

In connection with the high mortality of seedlings the following question arises: What are tha factors that determine the survival of some seedlings and the death of others? Experimental studies of the survival of psammophyte seedlings to a large extent confirmed M o r o z o w (1953) and S u k a č e v's (1953) earlier proposition concerning the differentiation of individuals into fit and less fit ones from the very beginning of their life. Even under standardized laboratory conditions seedlings that developed from seeds of the same size and at the same density differed in the rate of their growth and in their viability (S y m o n i d e s 1978b, cf. also R a b o t n o v 1950). R a b o t n o v (1950) suggests that under natural conditions individual differences between seedlings may result from the fact that prior to their germination the seeds remain in the soil for a variable length of time. According to the above-named author, soil properties may to a considerable degree affect the properties of the seeds and thereby the seedlings that emerge from them.

Irrespective of the individual differentiation of seedlings into weak and strong, under the conditions of a high density the sequence of emergence plays a very important role: the chance to survive belongs primarily to those seedlings which were the first to appear in the population and to occupy an appropriately large "living space" (Ross 1968 after H a r p e r 1977, R o s s and H a r p e r 1972, S y m o n i d e s 1978b).

3.5. CAUSES AND CONSEQUENCES OF AGGREGATED SPATIAL STRUCTURE OF SEEDLINGS

The seedlings of plants producing large numbers of diaspores and reproducing only generatively emerge in aggregations even when a considerable part of the biochore area is not covered with vegetation (S y m o n i d e s 1979a, 1979b). This type of spatial structure of seedlings naturally results in an aggregated distribution of adult individuals, which is common in the populations of the species under study (at least on a microscale), and in fact common in most plants regardless of their way of reproduction (K w i a t k o w s k a 1972, F a l i ń s k a 1976, W i l k o ń - M i c h a l s k a 1976, K w i a t k o w s k a and S y m o n i d e s 1978).

The direct cause of the aggregation of seedlings is an uneven distribution of diaspores in the soil; indirectly — it results from the micromosaic of habitats, and is also determined by the structure of the infructescences and diaspore dissemination mechanisms (H a r p e r 1961, H a r p e r, W i l l i a m s and S a g a r 1965, S y m o n i d e s 1978a).

The requirements as regards the minimum area in which the individual seedlings can grow vary with the species, and are to some extent dependent on the form of their growth. The rosette-shaped (of *Androsace septentrionalis*) and the tussock-shaped (of the grasses) seedlings naturally need more space for their growth than do the very small seedlings of *Cerastium semidecandrum*, or *Plantago indica*, hence the maximum seedling density in the aggregations depended on their size, the smaller the size, the higher the density (S y m o n i d e s 1979b, 1979c).

3.6. VIABILITY OF THE OFFSPRiNG OF VEGETATIVE ORIGIN

By contrast to the seedlings, the "vegetative offspring" is characterized by a much higher survivorship. In an extreme case, as in *Carex arenaria* (site 4), all individuals of the offspring survive until reproductive maturity; in the populations of the remainder of the species mortality of young individuals does not usually exceeds several per cent (S y m o n i d e s 1979a, 1979b). A low death risk of the progeny with vegetative reproduction is fairly common among many plant species (T a m m 1956, 1972, R a b o t n o v 1960b). H a r p e r (1967), and H a r p e r and O g d e n (1970) relate this to the high "reproductive effort" made by the plant to produce vegetative propagules.

As a result of the low mortality during the juvenile period, a considerable part of the vegetative offspring attains the reproductive maturity phase. With the generative reproduction — only a few per cent of the total number of seedlings survive till the fruiting. Because of the high mortality of seedlings, the average individual age in the populations of the species studied was much lower with generative reproduction than with vegetative reproduction (S y m o n i d e s 1979a, 1979b, 1979c).

3.7. ATTAINMENT OF THE REPRODUCTIVE MATURITY PHASE

In the populations of plants characterized by a very high mortality during the germination and establishment of seedlings, only a very small number of individuals usually die in later developmental phases. Among annuals, sometimes 100% of the individuals that have survived the seedling phase will live to attain the flowering and fruiting stages (S y m o n i d e s 1979b, cf. also Sharitz 1970 after H a r p e r 1977). A low mortality rate among adults (1–4%) was also found for populations of the perennials: *C. arenaria*, *K. glauca*, *F. psammophila*, propagating chiefly vegetatively. Only in very unfavourable conditions (expansion of *T. heterospermus* at site 7) will about 20% of individuals of this age group die. But even under such conditions the first to die are the youngest individuals, while adults survive for a much longer time (S y m o n i d e s 1979b, cf. also R a b o t n o v 1960b).

Regardless of the way of reproduction, the fraction of individuals of perennials attaining reproductive maturity is greater under less favourable habitat conditions when plant density is lower than under better conditions, as regards the nutrient supplies and water content in the sands, but with much of the ground surface being covered with vegetation. On the dry, unfixed sands of site 1 all the individuals of *Corynephorus canescens* which survived till the next growing season flowered and produced caryopses, while at site 3 — a small percentage of surviving tussocks did not attain the generative phase, while the remainder of them developed at a much slower rate. Similar relationships could be seen in *Festuca psammophila* and *F. duriuscula* in compact sods (S y m o n i d e s 1979a, 1979c). In certain situations, competition among individuals of the same species, or of different species more efficiently limits the growth of individuals than do the abiotic conditions of the environment (R a b o t n o v 1969, R a b o t n o v and S a u r i n a 1971).

3.8. SURVIVORSHIP CURVES OF THE POPULATIONS

The relationship between the death rate of the individuals of a population and their age and developmental stage is best represented by the survivorship curves. In plant populations (as in animal populations) individuals die according to three basic "types" (Deevey 1947):

Type I is characteristic of populations whose mortality — very low at the early stages of life — clearly grows with the age of the individuals. Its almost typical form could be seen in *C. arenaria*. Except for a small number of seedlings, for several years only senile individuals died: partially withered and with a lower ability to produce generative diaspores. The viability of young and fully mature shoots of *C. arenaria* is very high; even at sod edges bordering upon compact grassy vegetation, where the polycormones did not produce new individuals, the last, the youngest shoots survived to attain old age (S y m o n i d e s 1979b).

The low death risk in *C. arenaria* during the juvenile and the generative maturity periods probably results not only from a low reproductive capacity; most important is the spatial structure of the population, that is, a regular distribution of the individuals occupying a biochore. Because of this, and because of the great competitive power, no negative interaction of individuals could be seen in the population of this species, although such interaction usually occurs in the conditions of overcrowding and aggregated spatial structure (H a r p e r 1977).

The type I of survivorship curve has so far been only known from *Trichachne californica* Link (C a n f i e l d 1957), and several orchid species: *Dactylorchis incarnata* (L.) Verm., *D. sambucina* (L.) Verm., and *Orchis mascula* L. (T a m m 1972); however, it must be noted that orchid seedlings, which are very small, could have died without being noticed by the investigator.

If the death rate is constat throughout the life of the individuals, then the survivorship curve of a population is of Deevey's Type II (D e e v e y 1947), regardless of the age of the individuals. Mortality of this type was found in the *F. psammophila* population in the Festuco--Koelerietum glaucae patch (site 7) — under stabilized phytocenotic conditions (S y m o n i d e s 1979b). From the studies carriet out so far follows that a linear type of curve is often found for populations of perennial species propagating mainly vegetatively (T a m m 1972), although it also occurs in annuals in the case of an adverse factor acting continuously (Y o d a et al. 1963, S y m o n i d e s 1974). In some plants, an intensive mortality at the seedling stage is followed by type II of mortality. It is probable that the mortality of *Jasione montana* populations is of this type, although the material from which the curve has been drawn may have been insufficiently representative, because of the small number of seedlings recruited during the study period at site 9 (S y m o n i d e s 1979c).

However, characteristically similar was the mortality of a population of *Digitalis purpurea* L. It is thus possible that this is a common phenomenon among plants which, according to the conditions, are either biennial, or perennial (W e r n e r 1975, Oxley 1977 after H a r p e r 1977).

Type III of the survivorship curve is the most frequently encountered type. It indicates that the highest death rate takes place at early stages of the life of individuals. This type of mortality was followed by the populations of all the psammophyte species with generative type of reproduction (*Cerastium semidecandrum*, *Androsace septentrionalis*, *Tragopogon heterospermus*, *Corynephorus canescens*), in which an overcrowding of seedlings and of juvenile individuals was one of the common phenomena.

According to H a r p e r and W h i t e (1974), with generative reproduction and a high fecundity index there is always a large number of genotypes poorly adapted to the particular environmental conditions. Such individuals are eliminated from their population already at the earliest stages of their life. Another critical moment in the life of plants is the period of their intensive vegetative growth when the death risk increases again (H a w t h o r n 1974, S a r u k h á n 1974). A temporary decrease in vegetative growth taking place in the flowering phase accounts for the usually low death rate among the flowering plants, in spite of the

weakening caused by the "reproductive effort" (H a r p e r 1977). Hence during the flowering phase the populations attain a comparatively stable level of numbers; only in some species does the death risk increase again after flowering but before the attainment of physiological senility. This could be observed in *F. duriuscula*, the tussocks of which require more and more space as they grow in age.

An intermediate type of curve is peculiar to the population of *Koeleria glauca:* after a high death rate of the youngest individuals a clearly lower death probability is observed for several years, and then an increase occurs again during the old age. This seems to indicate a time distribution of the action of selection agencies which appear to be concentrated only at certain stages of the life of a plant (H a r p e r and W h i t e 1974).

In connection with the analysis of the survivorship curves several comments can be made:

1. In the case of vegetative reproduction, any type of curve depends on what we consider to be the individual of a population.

2. It is necessary to know the type of population survivorship curve to be able to correctly interpret the age pyramid; a pyramid with a broad base, indicating a dominance of young individuals in a population does not always unequivocally indicate a progressive, or expansive nature of the population. What is more, it can occur in retreating populations whose survival follows type III. In such cases, as has been demonstrated by studies, the production by the individuals that died represents a considerable percentage of the total biomass production (cf. M a t h e w s and W e s t l a k e 1969). Then inherent in the estimation of production from the maximum biomass will be a great error.

3.9. PLASTIC RESPONSES OF PSAMMOPHYTES TO POPULATION OVERCROWDING

These studies have shown that death and reproduction, the rate of attaining reproductive maturity, and the length of the life cycle are all closely interrelated. Under stabilized biotopic and phytocenotic conditions the populations maintain a relatively stable abundance, regardless of the type of reproduction (S y m o n i d e s 1979c). A low reproductiveness is usually associated with a low death rate (*F. psammophila, F. duriuscula, K. glauca, C. arenaria*), and a high progeny death risk, in the case of generative reproduction, is compensated for by a high "reproductive capacity" (*A. septentrionalis, C. semidecandrum, T. heterospermus, P. indica)*. Another characteristic feature is that in polycyclic perennials (regardless of the type of their reproduction) the juvenile phase is longer if the complete life period of the species is longer. In populations of the same species it is subject to some environmental modifications (cf. C h i p p i n d a l e 1948, C o o p e r 1948, R a b o t n o v 1969). This could be seen in *C. canescens* (on sites 1 and 3), and in *K. glauca* (on sites 6 and 7).

This does not mean, however, that the mechanisms regulating the abundance of a population in the system — population and its habitat — function with full efficiency. In plants, the tendency to increase the numbers of a population, peculiar to all living organisms, is not accompanied by a mortality that would fully balance the "excess" of individuals. Therefore under the conditions of a limited capacity of the environment plastic reactions — as a response to the overcrowding pressure — are one of the common phenomena, in addition to mortality. In this respect a greater diversity can be seen among the populations of plants reproducing generatively, which is understandable because of the greater probability of overcrowding.

The effect of density on the size and weight of individuals was particularly strongly marked in *P. indica*, but it could be seen also in *T. heterospermus, A. septentrionalis,* and in *C. semidecandrum* (S y m o n i d e s 1979b, 1979c).

In *P. indica*, very small numbers of individuals were sometimes lost due to mortality, although the density was high. Due to undernourishment, the plants were under-sized and had a very low weight which hardly balanced that of the individuals growing singly in the same unit area. A similar effect was also seen when individuals of both *Plantago indica* and *Salsola kali* contributed to the "overcrowding". In the unispecific system, and in a mixture of two different species – the important factor was primarily the total number of individuals inhabiting the same area (H a r p e r 1961). The "law of constant final yield" (S h i n o z a k i and K i r a 1956, Y o d a, K i r a and H o z u m i 1957) results from a limited biotope capacity, due to which a population (or a two-species system) forms an integrated system, where the growth possibilities of each individual depend on the resources at the disposal of the population (H a r p e r 1964a, 1964b, 1967).

Moreover, various investigations have proved that under conditions more favourable to the vegetative growth inter-individual competition is more intensive than under unfavourable conditions. This can be exemplified by the close, negative correlation between density and the size of *A. septentrionalis* individuals in years with an early spring, and almost a complete lack of this correlation when the life cycle of *A. septentrionalis* lasted a very short time, and all the individuals were small-sized (S y m o n i d e s 1979b).

All hitherto published studies indicate that all the factors responsible for the stimulation of the vegetative growth of plants at the same time enhance the competitive activity; they include the supplies of nutrients in the soil, water content in the soil, etc. (S u k a č e v 1928, Y o d a et al. 1963, W h i t e and H a r p e r 1970).

Under a strong pressure, inter-individual competition leads on to a situation where only few individuals grow exuberantly, while the size of the greater majority is below that of an "average" individual of the population. In such cases, the distribution of frequency in respect of the size of individuals is clearly asymmetric (positive skew), while the average size of an individual of a population is not at the same time the most frequently encountered one. Hierarchy among the individuals of a population was most evident in *Plantago indica* and *Cerastium semidecandrum*. K o y a m a and K i r a (1956) have demonstrated that a log-normal frequency distribution can occur also under natural conditions without density pressure, but overcrowding always increases this type of distribution.

A response to overcrowding, fairly common in the populations of the species under study, was a reduced production of fruit and diaspores. In the populations of *Androsace septentrionalis*, *Tragopogon heterospermus*, *Plantago indica*, and to a lesser extent also of *Corynephorus canescens*, this production was negatively correlated with the number of individuals per unit area (cf. H o d g s o n and B l a c k m a n 1957, B a k k e r 1960, P u c k- e r i d g e and D o n a l d 1967, P a l m b l a d 1968).

The effect of density on the size of individuals indirectly affects also the rate of their development and ability to attain the generative phases; this has been found for the populations of *T. heterospermus*, *J. montana* and *F. duriuscula* (S y m o n i d e s 1979b, 1979c; cf. also W e r n e r 1975 for *Dipsacus fullonum* L.). Regardless of their age, plants below a certain limit of minimum size did not produce flowers; they characteristically lived for a longer time than did those which flowered early (cf. also H o l t 1972).

In very compact communities the correlation between the size of the plants and the attainment by them of the generative phases existed also in *F. duriuscula* and *F. psammophila*. Within very strong compact clones a certain number of individuals "vegetated" for several years in a state of vegetative and generative "underdevelopment" (S y m o n i d e s 1979c). In such cases, the age structure of a population cannot be inferred from the structure of the population

as described on the basis of the sizes and developmental stages of the individuals, for individuals of the same age may vary in size, and in the stage of generative and vegetative maturity.

By contrast to perennials, which usually respond to density pressure by a delay in the development of their individuals, in the populations of annuals an acceleration of growth is usually observed. This problem has been discussed in more detail in a previous paper (S y m o n i d e s 1978c).

4. FINAL REMARKS

In the summing-up of the discussion it may be stated that an approach to the plant association as being an assemblage of populations of different species, and a detailed study of population phenomena make possible an insight into the relations existing in plant communities, in order to better understand their structure, inner dynamics, and tendencies and growth processes. The studies of populations allow also to evaluate the role of particular species with the succession of communities.

It is known from studies that in the initial phases of the development of plant communities the main role is played by those species: (a) whose populations are capable of fast spreading and efficiently increasing their numbers; (b) whose high fecundity and at the same time a fast turnover of individuals determine a fast transformation of the biotope by enriching infertile sands with organic matter; (c) which because of their aggregated spatial structure, create in their vicinity, already at an early stage of population formation, a specific microclimate which is more favourable also for those species that enter at a later stage.

In the period when free growth and development of plants are limited primarily by the severe external conditions, there is practically no noticeable inter-individual competition; what is more, it is only due to their mutual spatial proximity that the individuals can survive. It is the life activity of the pioneer plants that initiates also the spatial biotope diversification, which becomes intensified with the development of communities.

The diversity of an initial community is manifested only by individual variation, i.e., morphological differences between individuals of the same age, but gradually there also occurs an increasing differentiation in respect of the growth phases and individual age. This is followed by the differentiation of the action on the environment and of the utilization of its resources. The appearance of further species is accompanied by the appearance of the initial stage biocenotic relations. The diversity of growth forms, phenology, utilization of all types of environment leads on to a gradual differentiation of niches and their gradual filling. Gradually, too, there appear interactions between populations of different species, in addition to intra-populational interactions. They to a large degree determine the occurrence and abundance of the populations of the particular species. Due to the deterioration of the conditions affecting the growth and development of seedlings, it is primarily the populations of perennials, at the same time able to reproduce vegetatively, that have the chance to stay in compact phytocenoses, and have a high dynamic value. A low mortality of the offspring in such populations, the possibility to produce offsprings many times, as well as the longevity of the plants make it possible for the system to attain stability.

5. SUMMARY

The paper discusses the results of studies concerned with changes in psammophyte vegetation on an inland dune in the process of being overgrown, and selected population properties of selected psammophyte species (S y m o n i d e s 1979a, 1979b, 1979c). The studies have shown that only a small number of species possess the ability to occupy extremely dry and infertile dune habitats. This is mainly because of the conditions which are unfavourable for germination and growth of seedlings (cf. A y y a d 1973, S h a r m a 1973, 1976). In the process of bare sand colonization an important role is played by the settlement of *Corynephorus canescens* tussocks which initiate the formation of a pioneer population of initial communities, and the process of dune overgrowing. Species selection is effected from the very beginning of the formation of the initial communities in extreme habitats.

In the course of dune overgrowing, plant communities consist of long-living species with a strongly developed root system, and able to reproduce vegetatively. In very compact communities, the small number of populations of annuals present there represent early-spring plants, whose life cycle is completed before the phenologically later perennials start their growth.

During the development of plant communities, the basic population reaction to changes in the phytocenotic and biotopic conditions is a growth or decrease in numbers, or maintenance of a relative abundance equilibrium. Reproductive efficiency depends to a large extent on the type of reproduction, this being subject to strong environmental modifications (H a r p e r and W h i t e 1971, Z a u g o l n o v a 1972, F a l i ń s k a 1976, 1977, H a r p e r 1977, and others). The transition from generative to vegetative reproduction, observed in the same species in the course of dune overgrowing, is gradual (*Festuca psammophila, F. duriuscula, Koeleria glauca*), or it is only during the invasion that a growth in numbers is accomplished through generative reproduction (*Carex arenaria, Hieracium pilosella, Thymus serpyllum*).

Regardless of the way of reproduction, psammophytes produce a large number of diaspores, this being a characteristic feature of the plants of open communities (S a l i s b u r y 1942, 1952, W i l k o ń - - M i c h a l s k a 1976). A considerable proportion of the diaspores remain accumulated in the surface sand layers, and only a small percentage of them germinate (K r o p a č 1966, N a y l o r 1972a, 1972b), this being especially true of very compact communities. However, the real number of the seeds that germinate is greater than can be estimated from the number of seedlings, but the majority of germs die before emerging above the ground (cf. B l a c k 1956, 1963, G r i m e and J e f f r e y 1965, R o s s and H a r p e r 1972, S y m o n i d e s 1979b). The existence of conditions unfavourable for the germination of diaspores, and a high mortality of individuals at the earliest stages of life account for the great diaspore "overproduction".

Psammophyte seedlings usually grow in aggregations, which, on the one hand, increases the competition for space and food, and, on the other hand, increases their survivorship under extreme conditions (cf. Y o d a et al. 1963, M a r s c h a l l and J a i n 1969, S y m o n i d e s 1977). A higher death rate of the seedlings in populations of polycyclic species, especially those capable of vegetative reproduction, relative to the populations of monocyclic species, confirms the opinion that the "strategy" and "tactics" of the annuals and perennials are different (H a r p e r and O g d e n 1970, F a l i ń s k a 1977). The death of some seedlings and survival of others depend on: (1) their individual differentiation into fitter and less fit ones (M o r o z o w 1953, S u k a č e v 1953, S y m o n i d e s 1978b), (2) density (H a r p e r and C h a n c e l l o r 1959, Z a r z y c k i 1965), (3) the length of the time spent in the soil by the diaspores from which the seedlings develop (R a b o t n o v 1950), (4) the sequence of coming-up (R o s s and H a r p e r 1972, S y m o n i d e s 1977), (5) environmental conditions (W i l k o ń - M i c h a l s k a 1976, F a l i ń s k a 1977). Vegetative progeny is characterized by a much higher survival rate; H a r p e r (1967) relates this to the great reproductive effort associated with vegetative propagation.

The viability of the individuals of a population varies with their age, and it depends also on the abiotic and biotic conditions. The populations of the psammophytes studied were characterized by different survivorship curves: type I was peculiar to *C. arenaria* in which mortality affects primarily the senile individuals, and almost 100% of the progeny survives till the reproductive age (cf. C a n f i e l d 1957, T a m m 1972); a constant death risk throughout the life period (type II) was recorded for *F. psammophila*. This type of mortality is characteristic of the populations of perennials, or annuals if there is continuous action of an adverse factor (Y o d a et al. 1963, S y m o n i d e s 1974). Type III survivorship curve is the most frequently encountered type, where most of the individuals affected by mortality die at an early stage of their life; this type was represented by *Androsace septentrionalis, C. canescens* and other species reproducing by seeds (cf. H a w t h o r n 1974, S a r u k h á n 1974).

Although mortality usually eliminates a considerable number of individuals, in cases of high reproductiveness overcrowding was found to be a common phenomenon in the populations of the species studied, as well as — in response to the overcrowding pressure — plastic reactions of the plants. These were manifested by a reduced size, a decreased biomass production and diaspore production, by a retarded (perennials), or accelerated (annuals) development, etc., that is, reactions which commonly occur in the populations of many species found in different ecosystems (S h i n o z a k i and K i r a 1956, Y o d a, K i r a and H o z u m i 1957, H a r p e r 1961, 1967, P a l m b l a d 1968, and others), and are connected with intra- and interspecific competition.

6. POLISH SUMMARY

W pracy przedyskutowano wyniki badań dotyczących przemian roślinności psammofilnej na zarastającej wydmie śródlądowej oraz populacyjnych właściwości wybranych gatunków psammofilnych (S y m o n i d e s 1979a, 1979b, 1979c). Badania wykazały, że zdolność zajmowania skrajnie suchych i jałowych siedlisk wydmowych ma niewielka liczba gatunków, przede wszystkim ze względu na niekorzystne warunki do kiełkowania i wzrostu siewek (por. A y y a d 1973, S h a r m a 1973, 1976). W procesie zasiedlania nagich piasków poważną rolę odgrywa osiedlenie się pionierskich kęp Corynephorus canescens, które zapoczątkowują formowanie się pionierskiej populacji inicjalnych zbiorowisk i proces zarastania wydmy. Dobór gatunków na siedliskach skrajnych dokonuje się od samego początku kształtowania się inicjalnych zbiorowisk.

W toku zarastania wydmy w skład zbiorowisk roślinnych wchodzą gatunki zdolne do wegetatywnej reprodukcji, długo żyjące, z silnie rozwiniętym systemem korzeniowym. Nieliczne populacje gatunków jednorocznych w zbiorowiskach silnie zwartych należą do roślin wczesnowiosennych, które zamykają swój cykl życiowy zanim rozpoczną wegetację późniejsze fenologicznie rośliny trwałe.

Podstawową reakcją populacyjną na zmiany warunków fitocenotycznych i biotopowych w miarę rozwoju zbiorowisk roślinnych jest wzrost, spadek lub też utrzymanie względnej równowagi liczebności. Efektywność reprodukcji w znacznej mierze zależy od sposobu rozmnażania, który podlega silnym modyfikacjom środowiskowym (H a r p e r i W h i t e 1971, Z a u g o l n o v a 1972, F a l i ń s k a 1976, 1977, H a r p e r 1977 i inni). Przejście z generatywnego na wegetatywny typ reprodukcji, obserwowany u tych samych gatunków w toku zarastania wydmy, odbywa się stopniowo (Festuca psammophila, F. duriuscula, Koeleria glauca), albo też tylko w okresie inwazji wzrost liczebności populacji następuje dzięki rozmnażaniu generatywnemu (Carex arenaria, Hieracium pilosella, Thymus serpyllum).

Niezależnie od sposobu reprodukcji psammofity produkują dużą liczbę diaspor, co jest charakterystyczne dla roślin otwartych zbiorowisk (S a l i s b u r y 1942, 1952, W i l k o ń - M i c h a l s k a 1976). Znaczna część diaspor zalega w powierzchniowych warstwach piasków; kiełkuje nieznaczny procent (K r o p a č 1966, N a y l o r 1972a, 1972b), zwłaszcza w silnie zwartych zbiorowiskach. Prawdopodobnie liczba rzeczywiście skiełkowanych nasion jest jednak większa, niż można by sądzić na podstawie liczby siewek, ale większość kiełków ginie, zanim zdążą wyrosnąć ponad powierzchnię gleby (por. B l a c k 1956, 1963, G r i m e i J e f f r e y 1965, R o s s i H a r p e r 1972, S y m o n i d e s 1978b). Niekorzystne warunki do kiełkowania diaspor i wysoka śmiertelność osobników w najwcześniejszych okresach życia tłumaczą zjawisko ogromnej „nadprodukcji" diaspor.

Siewki psammofitów wyrastają zwykle w skupiskach, co z jednej strony zwiększa między nimi konkurencję o przestrzeń i pokarm, z drugiej jednak — w warunkach skrajnych — przyczynia się do ich przeżywania (por. Y o d a et al. 1963, M a r s c h a l l i J a i n 1969, S y m o n i d e s 1977). Intensywniejsze wymieranie siewek w populacjach gatunków policyklicznych, zwłaszcza zdolnych do wegetatywnej reprodukcji, w porównaniu z populacjami gatunków monocyklicznych, potwierdza odmienną „strategię" i „taktykę" roślin jednorocznych i wieloletnich (H a r p e r i O g d e n 1970, F a l i ń s k a 1977). Wymieranie jednych siewek a przeżywanie innych zależy od: 1) ich zróżnicowania osobniczego na słabsze i silniejsze (M o r o z o w 1953, S u k a č e v 1953, S y m o n i d e s 1978b), 2) zagęszczenia (H a r p e r i C h a n c e l l o r 1959, Z a r z y c k i 1965), 3) długości okresu przebywania diaspor w glebie, z których te siewki wyrosły (R a b o t n o v 1950), 4) sekwencji wyrastania (R o s s i H a r p e r 1972, S y m o n i d e s 1977), 5) warunków środowiskowych (W i l k o ń - M i c h a l s k a 1976, F a l i ń s k a 1977). Potomstwo wegetatywne cechuje znacznie wyższa przeżywalność; H a r p e r (1967) wiąże to z dużym wysiłkiem reprodukcyjnym przy pomnażaniu wegetatywnym.

Żywotność osobników w populacji zmienia się wraz z ich wiekiem, zależy także od układu warunków abiotycznych i biotycznych. Populacje badanych psammofitów charakteryzowały się różnymi typami

krzywych przeżywania: typ I charakteryzował *C. arenaria*, u której giną przede wszystkim osobniki senilne, natomiast potomstwo przeżywa do wieku reprodukcji niemal w 100% (por. C a n f i e l d 1957, T a m m 1972); stałe ryzyko śmierci w ciągu całego życia (typ II) wykazała *F. psammophila*. Taki typ wymierania charakteryzuje populacje gatunków wieloletnich lub też jednorocznych, jeśli zaznacza się ciągłe oddziaływanie niekorzystnego czynnika (Y o d a et al. 1963, S y m o n i d e s 1974). Najczęściej spotykanym wśród roślin jest typ III krzywej przeżywania, w którym większość wymierających osobników ginie we wczesnym okresie życia; ten typ reprezentowały *Androsace septentrionalis, C. canescens* i inne gatunki reprodukujące się z nasion (por. H a w t h o r n 1974, S a r u k h á n 1974).

Mimo iż śmiertelność redukuje zazwyczaj znaczną liczbę osobników, to jednak w przypadku wysokiej rozrodczości do powszechnych zjawisk w populacjach badanych gatunków należało przegęszczenie i — w odpowiedzi na presję przegęszczenia — plastyczne reakcje roślin. Wyrażały się one w obniżonym wzroście, produkcji biomasy, produkcji diaspor, w opóźnionym (u roślin wieloletnich) lub przyspieszonym (u jednorocznych) rozwoju itp. Są to reakcje powszechnie występujące w populacjach wielu gatunków z różnych ekosystemów (S h i n o z a k i i K i r a 1956, Y o d a, K i r a i H o z u m i 1957, H a r p e r 1961, 1967, P a l m b l a d 1968 i inni), związane z oddziaływaniem konkurencji wewnątrz- i międzygatunkowej.

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