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NUMBERS, DISTRIBUTION AND SPECIFIC COMPOSITION OF DIASPORES IN THE SOILS OF THE PLANT ASSOCIATION SPERGULO-CORYNEPHORETUM

ABSTRACT: The number, distribution (vertical and horizontal) and the specific composition of diaspores in dune sands were studied in two time periods of the growing season. It has been found that in spite of the high rate of diaspore production by the psammophytes, the number of diaspores in the soils of the community under study was fairly low, whereas their specific composition was much richer than that of the vegetation of the patch investigated. The diaspores, which were found to be primarily located in the surface layers of the soil, showed a clearly clumped type of distribution. They appeared to be accumulated first of all in local depressions and where there were aggregations of mature individuals. During the growing season the total number of diaspores and the quantitative relations between the diaspores of the particular species varied.

KEY WORDS: Dune sands, Spergulo-Corynephoretum, psammophytes, diaspores, numbers, specific composition, distribution in the soils.

Contents

1. INTRODUCTION

The present paper is a kind of supplement to the researches into the survival and mortality of seedlings in dune plant populations (S y m o n i d e s 1977). The researches have revealed,

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among other things, that the seedlings of most species grow in larger or smaller clumps, leaving quite empty areas close by. A question therefore arises as to whether the clumped distribution of seedlings is the result of the same type of spatial distribution of diaspores in the soil, or whether seeds are evenly distributed in soil and the clumped distribution results from the action of some other factors. Among the possible factors the following can be enumerated: the microrelief and, associated with it, the "number of safe places for germination" (Harper, Williams and Sagar 1965), an uneven distribution of nutrient components (Snaydon 1962), as well as the soil moistness, which shows a characteristic mosaic nature (Wilkoń-Michalska and Symonides 1974), being in certain places sufficient for the germination of seeds and not sufficient in other places.

Another interesting problem emerged from the fact that the seedlings of some species occur abundantly every year, while those of other species – with a similar rate of diaspore production and in similar habitats – are always found in very small numbers, or do not occur in a community at all. A low numeric level of seedlings may in fact be connected solely with a low capacity of the seeds to germinate, but it may also result from, for example, the diaspores being carried outside the boundaries of a community (that is their absence from the soils), or washed into deeper soil layers by rain waters, where they lose the opportunity to germinate (Pawłowski and Zarzycki 1972).

It was with the aim to try to at least partially elucidate these problems that the analysis of the specific composition, numbers and distribution of diaspores in sand dunes has been carried out. It should be emphasized that the problem of seed content in the soils of natural vegetation communities has so far been little studied. Most information on this subject has been supplied by Rabotnov's (1954, 1960) papers concerning various meadow associations. Some information, as a matter of fact fairly general, can be found in the papers by Salisbury (1942) and Barbour and Lange (1967). In Poland, studies of the number and species composition of the diaspores in the soils of the Carpathian beechwood have been carried out by Zarzycki (1964).

2. STUDY AIMS AND METHODS

The investigations were carried out in a large patch of the association Spergulo-Corynephoretum (Tx. 1928) Libb. 1933 in the Basin of Toruń. A floristic list of the patch is presented in Table I. A more detailed description of the study area can be found in the paper by Symonides (1974).

Soil samples for analyses were collected twice: in the August of 1973, between the period of fructification and dissemination of most of the species present in the study area and still before the germination of the seeds of two species which are dominant in the patch: *Spergula vernalis* and *Corynephorus canescens;* the second date was established for the spring of the next year, following the winter rest period.

To determine the specific composition, the number, and the spatial distribution of diaspores, both vertical and horizontal, the method of random samples was used. Samples were collected in areas demarcated by 100 throws of a rectangular frame of the size 10 × 20 cm. The soil layers, cut-off at 2 cm intervals down to a total depth of 20 cm, were poured into plastic bags, each with a consecutive number of sample.

Apart from the above, a method of predetermined collecting of samples was used in order to establish any possible effects of the distance from the fructifying mature individuals, and the

effect of the microrelief on the diaspore content in the surface layers of soil, i.e., from 0 to 2 cm, and from 2 to 4 cm. In this case the samples were collected at 5 cm intervals over the distance from *Corynephorus canescens* tussocks and from clumps, dying at this time of the year, of *Spergula vernalis* individuals. For this purpose 10 grass tussocks and 10 patches with the spring spurry were taken into account. To establish the number of diaspores in the dune sands with different relief, soil samples were collected at sites deprived of the vegetation cover — 30 samples were collected from each depression, flat site and elevation; the depressions and elevations were small elements of the "microrelief" of the patch under study, th their diameter not exceeding 40 cm.

The total number of samples collected for the analyses was 2,380. Air-dry soil samples were sieved using soil sieves of different mesh diameters. The diaspores were identified and counted separately in each sample. For six species, dominating in respect of the percentage of their diaspores in the soils of the community studied and at the same time being components of the association, in the autumn of 1974 an assessment was made of the germinating capacity of seeds found in the top layers of the soil. The seeds were sown in Petri dishes, 100 seeds in each dish, in four replications for each species. After 4 weeks the germs were counted; seeds of species with a low germinating power were kept in the dishes for another month and then the average germination per cent of seeds of each of the species was calculated.

3. RESULTS AND DISCUSSION

The number of diaspores found in the soils of Spergulo-Corynephoretum, and belonging to the species that made up the community (Table I), appeared to be much smaller than could be

Table I. Floristic composition of the study patch and the numbers of flower species diaspores (per 1 m^2 soil)

Species list	Quantitative and structural relations*	Number of diaspores	
		24 August 1973	7 April 1974
Flower species:			
Corynephorus canescens (L.) P. B.	2.2	1,312	607
Spergula vernalis Willd.	2.3	1,407	1,021
Festuca psammophila Hack.	+	188	82
Koeleria glauca (Schkuhr) DC.	+	131	71
Helichrysum arenarium (L.) Moench	+	147	37
Tragopogon heterospormus Schweigg.	+	136	44
Scleranthus perennis L.	+	49	48
Hieracium pilosella L.	+	41	27
		total of diaspores	
		3,411	1,937
Sporophyte species:			
Polytrichum piliferum Schreb.	2.2		
Cladonia silvatica (L.) Harm.	1.2		
Cornicularia aculeata (Schreb.) Ach.	+		

*According to the scale of Braun-Blanquet (Scamoni 1967).

expected on the basis of the high individual production of diaspores. For instance, under favourable weather conditions in the study area a shapely individual of *Spergula vernalis* produces over 600 seeds (S y m o n i d e s 1974), and individual of *Tragopogon heterospermus* 2,500–3,000 diaspores, whereas a large tussock of *Corynephorus canescens* produces about 2,000 caryopses (E. Symonides – unpublished data). For the last named species M a r s h a l l (1967) reported much larger numbers, namely up to 36,000 caryopses per a shapely tussock of dubawngrass.

Table II. Number of diaspores in individual soil layers per 1 m^2

Depth (in cm)	24 August 1973	7 April 1974
0–2	2,350	289
2–4	690	1,095
4–6	227	385
6–8	110	223
8–10	87	79
10–12	45	75
12–14	27	33
14–16	1	2
16–18	0	0
18–20	0	1
Total	3,537	2,182

A slightly larger total number of diaspores in a soil profile (Table II) indicates an insignificant admixture of seeds belonging to species from outside the Spergulo-Corynephoretum patch. It should be noted here that the numbers contained in Table II relate only to fully developed diaspores; apart from this, in August there were 825, and in April 1,053 damaged, or not fully developed diaspores.

The small numbers of diaspores present in dune sands seem to result from two causes: (1) the open ground and the poor vegetation, which does not hold back the diaspores, these being usually light in the psammophytes, and (2) the times of fructification and dissemination of most dune plant species which occur in June and July. With the fairly high air temperature and a small amount of rainfall, even weak winds cause re-winnowing and dislocation of whole sandbanks, with the diaspores in them, over considerable distances. The winnowing of diaspores from poorly overgrown and poorly fixed sands would thus be the main cause of their low content in the soils investigated. This conclusion is proved by the comparison of the results obtained with the data reported by R a b o t n o v (1954, 1960), who gives numbers from 1,500 up to 27,000 per 1 m^2 of different meadow communities (with a continuous vegetation), or by Z a r z y c k i (1964), according to whom in the Carpathian beechwood soils 1,700 up to 2,000 undamaged and about 700 damaged diaspores can be found (per 1 m^2). Considering the diaspore production by the forest species (F a l i ń s k a 1968), these are rather large numbers.

The specific composition and quantitative relations between the diaspores of the individual species in two surface soil layers have been presented in Figures 1 and 2. Because of the minimal number of their diaspores, the following fourteen species are not represented in these figures by separate hachures, but are given under a common symbol *15: Armeria elongata* (Hoffm.) Koch, *Bromus tectorum* L., *Carex hirta* L., *Dianthus carthussianorum* L., *Erigeron*

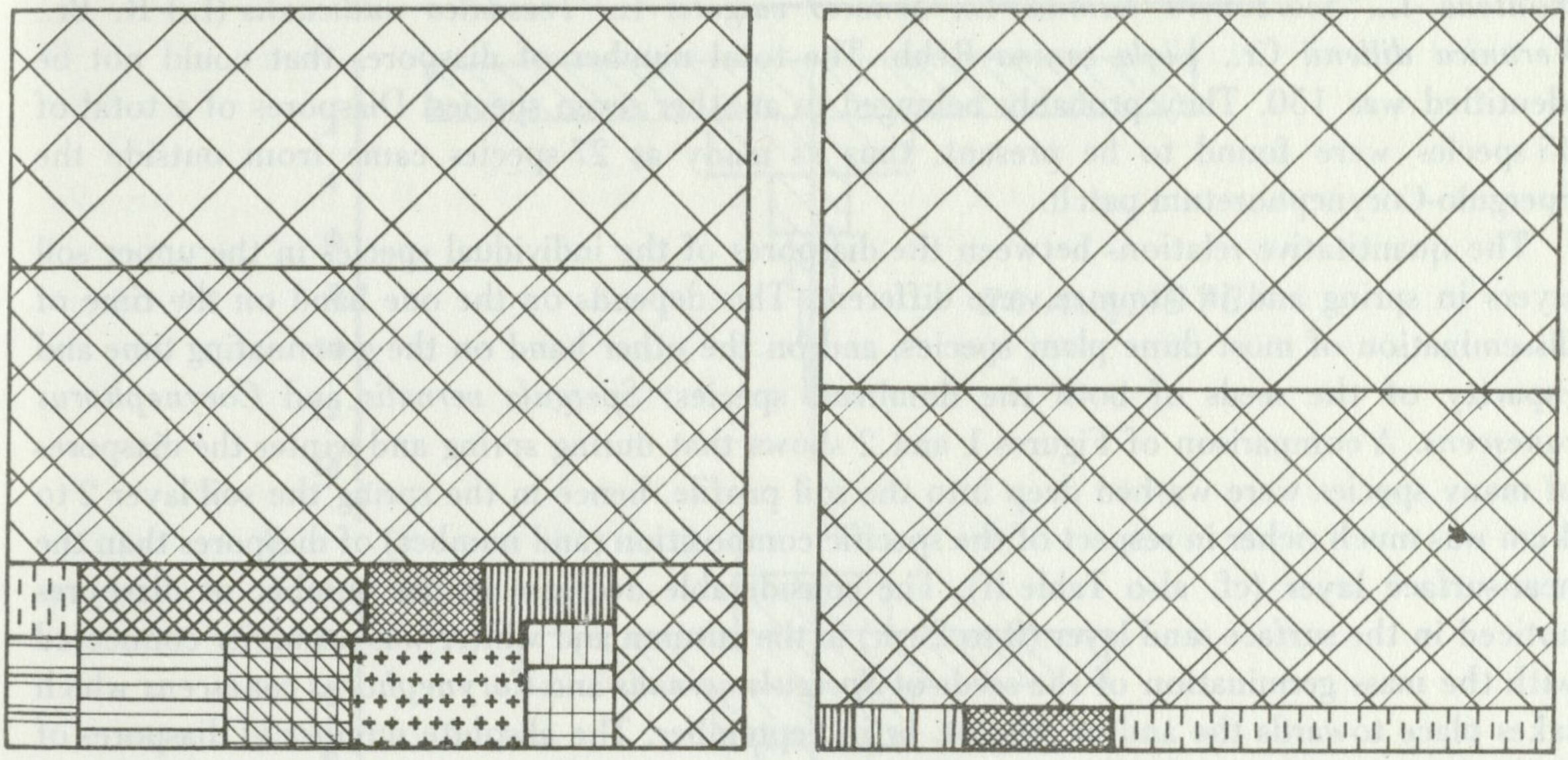

Fig. 1. Percentage contribution of diaspores of individual species at the depth 0–2 cm (left side) and 2–4 cm (right side); 24 August 1973
For explanations see Figure 2

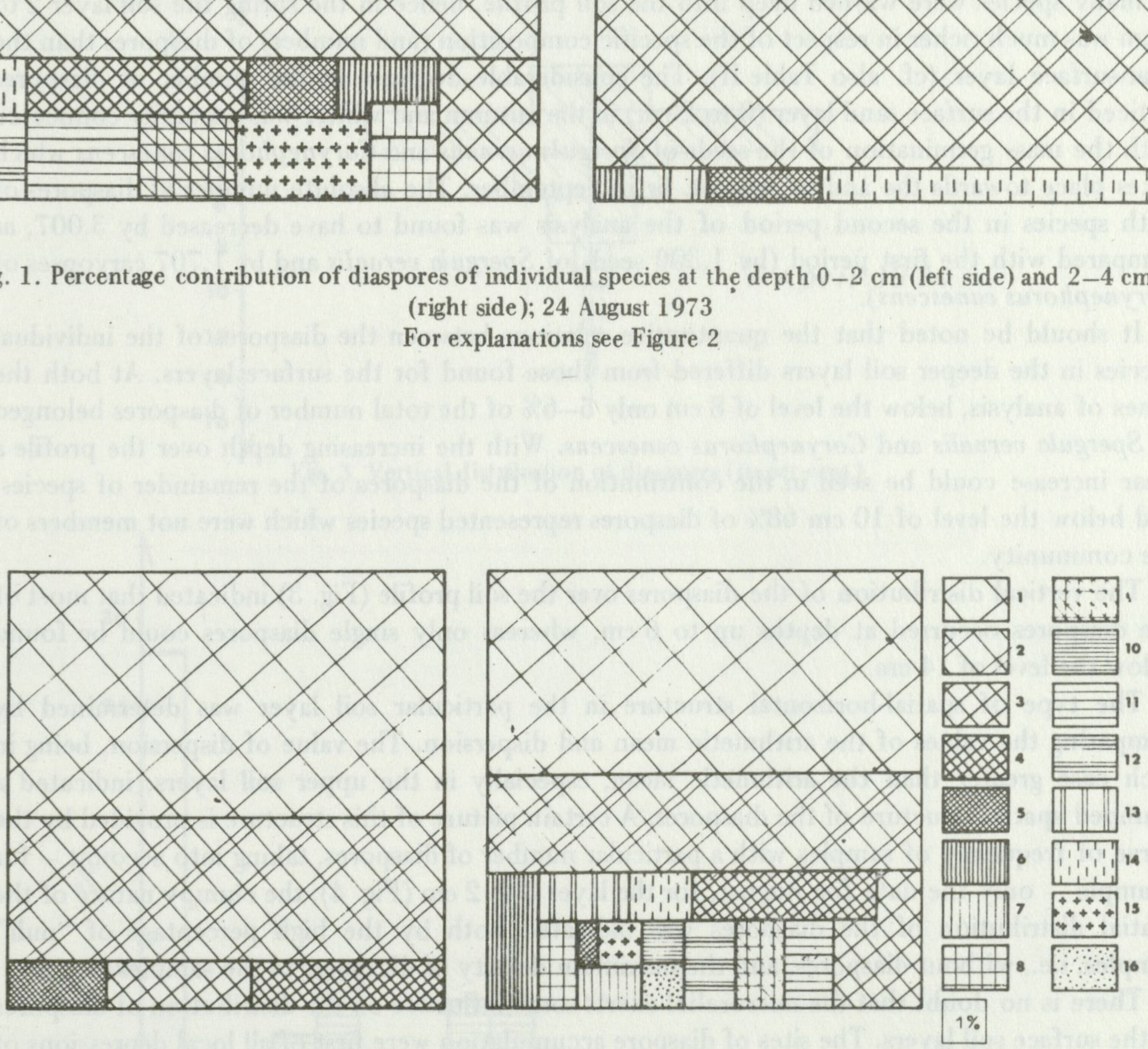

Fig. 2. Percentage contribution of diaspores of individual species at the depth 0–2 cm (left side) and 2–4 cm (right side); 7 April 1974
1 – *Spergula vernalis*, *2* – *Corynephorus canescens*, *3* – *Festuca psammophila*, *4* – *Koeleria glauca*, *5* – *Helichrysum arenarium*, *6* – *Scleranthus perennis*, *7* – *Salsola kali* L., *8* – *Digitaria sanguinalis* (L.) Scop., *9* – *Pinus silvestris* L., *10* – *Pulsatilla pratensis* (L.) Mill., *11* – *Tragopogon heterospermus*, *12* – *Plantago indica* L., *13* – *Carex arenaria* L., *14* – *Hieracium pilosella*, *15* – fourteen species, listed in the text, *16* – species which could not be identified

canadensis L., *Filago minima* (Sm.) Fr., *Gypsophila fastigiata* L., *Herniaria glabra* L., *Jasione montana* L., *Scorzonera humilis* L., *Senecio vulgaris* L., *Teesdalea nudicaulis* (L.) R. Br., *Veronica dillenii* Cr., *Viola canina* Rchb. The total number of diaspores that could not be identified was 150. They probably belonged to another seven species. Diaspores of a total of 35 species were found to be present, thus as many as 27 species came from outside the Spergulo-Corynephoretum patch.

The quantitative relations between the diaspores of the individual species in the upper soil layers in spring and in summer were different. This depends on the one hand on the time of dissemination of most dune plant species, and on the other hand on the germinating time and capacity of the seeds of both the dominant species: *Spergula vernalis* and *Corynephorus canescens*. A comparison of Figures 1 and 2 shows that during spring and winter the diaspores of many species were washed deep into the soil profile, hence in the spring the soil layer 2 to 4 cm was much richer in respect of the specific composition (and number) of diaspores than the near-surface layer (cf. also Table II). The considerable decrease in the number of diaspores noticed in the surface sand layer (0 to 2 cm) in the autumn and winter was primarily connected with the mass germination of the seeds of *Spergula vernalis* and *Corynephorus canescens* which takes place towards the and of August, or in September. The absolute number of diaspores of both species in the second period of the analysis was found to have decreased by 3,007, as compared with the first period (by 1,300 seeds of *Spergula vernalis* and by 1,707 caryopses of *Corynephorus canescens*).

It should be noted that the quantitative relations between the diaspores of the individual species in the deeper soil layers differed from those found for the surface layers. At both the times of analysis, below the level of 8 cm only 5–6% of the total number of diaspores belonged to *Spergula vernalis* and *Corynephorus canescens*. With the increasing depth over the profile a clear increase could be seen in the contribution of the diaspores of the remainder of species, and below the level of 10 cm 68% of diaspores represented species which were not members of the community.

The vertical distribution of the diaspores over the soil profile (Fig. 3) indicated that most of the diaspores occurred at depths up to 6 cm, whereas only single diaspores could be found below the level of 14 cm.

The type of spatial-horizontal structure in the particular soil layer was determined by comparing the values of the arithmetic mean and dispersion. The value of dispersion, being in each case greater than the arithmetic mean, especially in the upper soil layers, indicated a clumped spatial structure of the diaspores. A certain picture of this structure is provided by the curve of frequency of samples with a particular number of diaspores, taking into account – for example – only the data for August, for the layer 0 to 2 cm (Fig. 4); the clumpy nature of the spatial distribution of the diaspores was indicated both by the high percentage of "null" samples, i.e., without diaspores, and the maximum density of diaspores in the samples.

There is no doubt that the microrelief exerts some influence on the distribution of diaspores in the surface soil layers. The sites of diaspore accumulation were first of all local depressions of the terrain (Fig. 5), winnowing from which is rather difficult. Also, part of the diaspores found in the depressions had been carried into them by the rain water, washing away the light, small seeds of the psammophytes from the surface of the bare sands.

The results of the investigations have also confirmed the assumption that there occurs a relationship between the number of diaspores present in the surface soil layers and the distance from the fructifying individuals. A larger number of diaspores found in the immediate vicinity of the individuals that produce them (Figs. 6, 7) not only results from the fact that even light

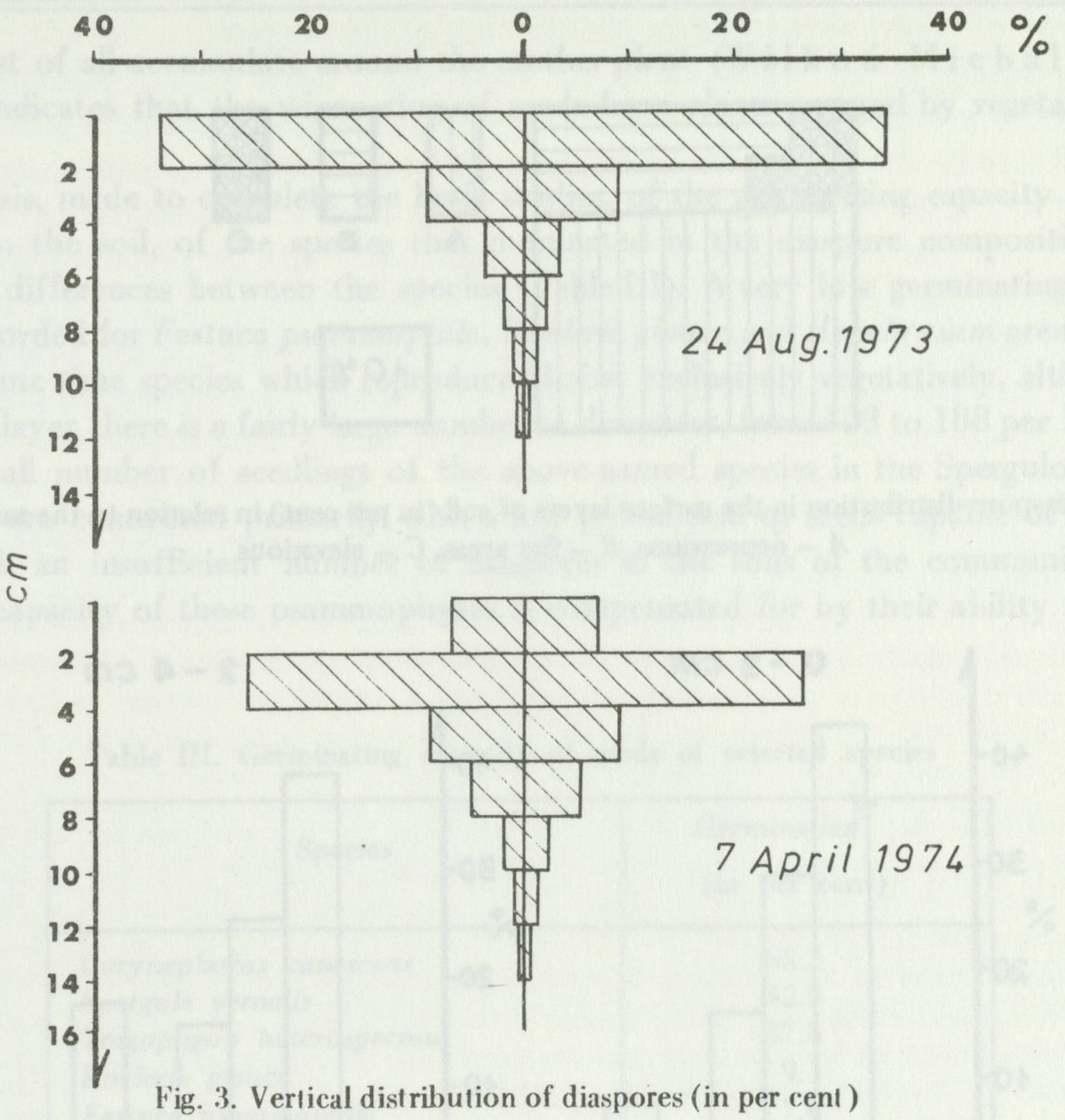

Fig. 3. Vertical distribution of diaspores (in per cent)

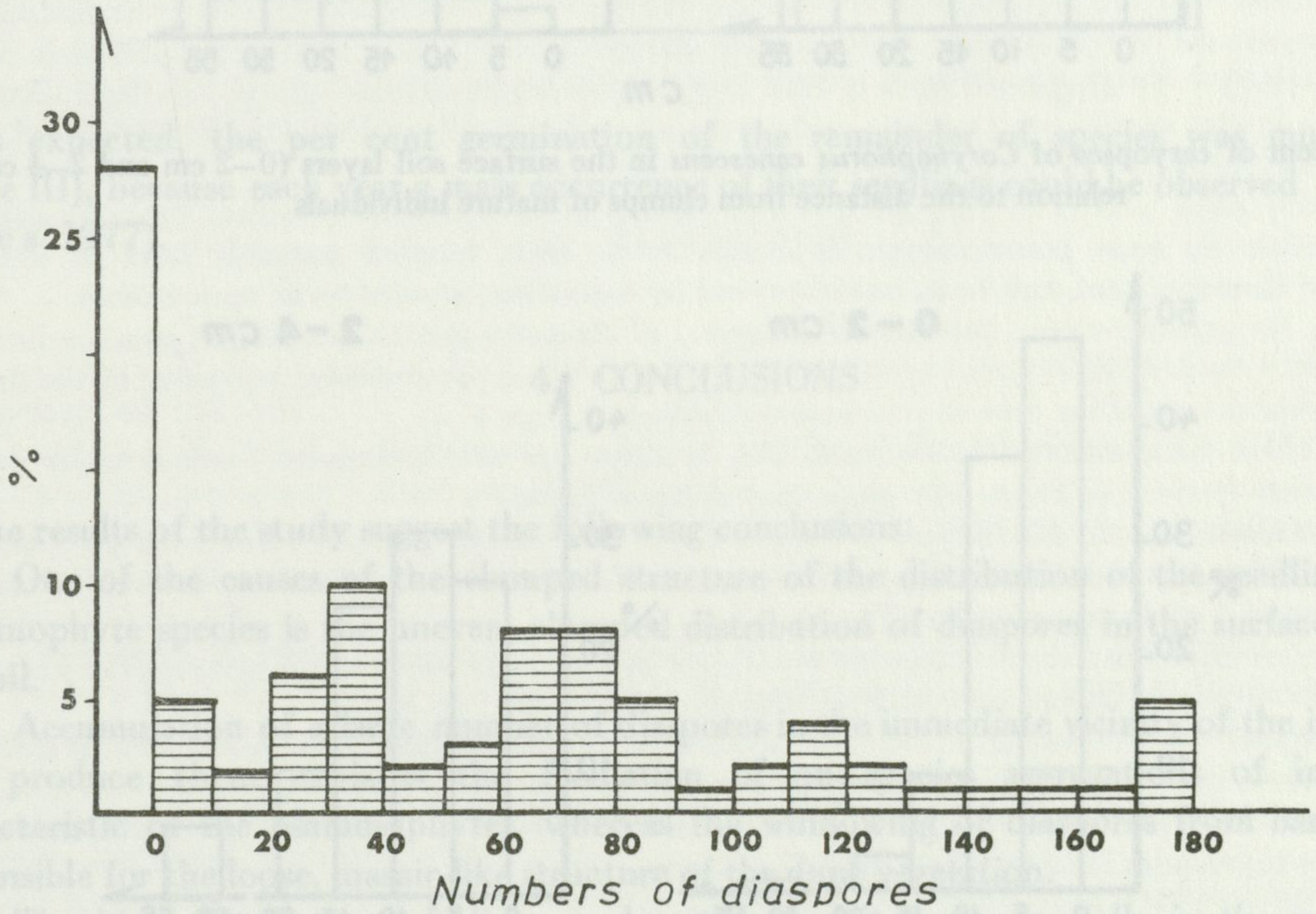

Fig. 4. Frequency of samples (in per cent) with different numbers of diaspores
Empty column – samples without diaspores

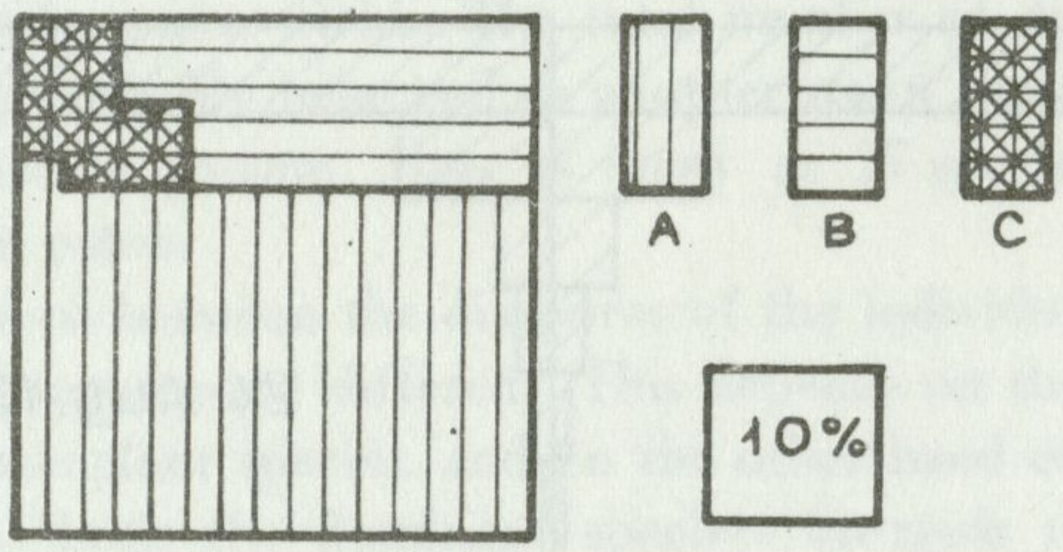

Fig. 5. Diaspore distribution in the surface layers of soil (in per cent) in relation to the microrelief
A – depressions, *B* – flat areas, *C* – elevations

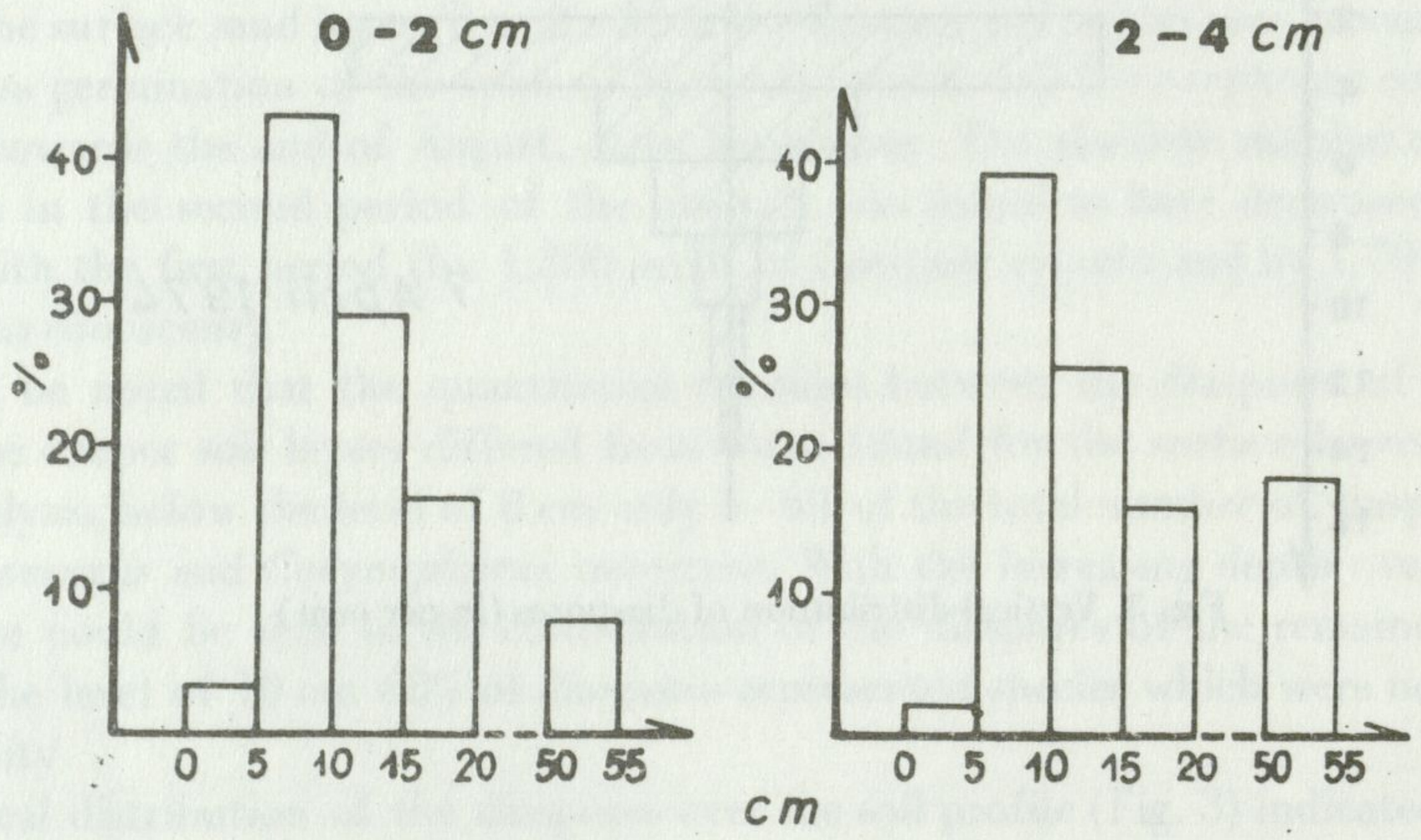

Fig. 6. Per cent of caryopses of *Corynephorus canescens* in the surface soil layers (0–2 cm and 2–4 cm) in relation to the distance from clumps of mature individuals

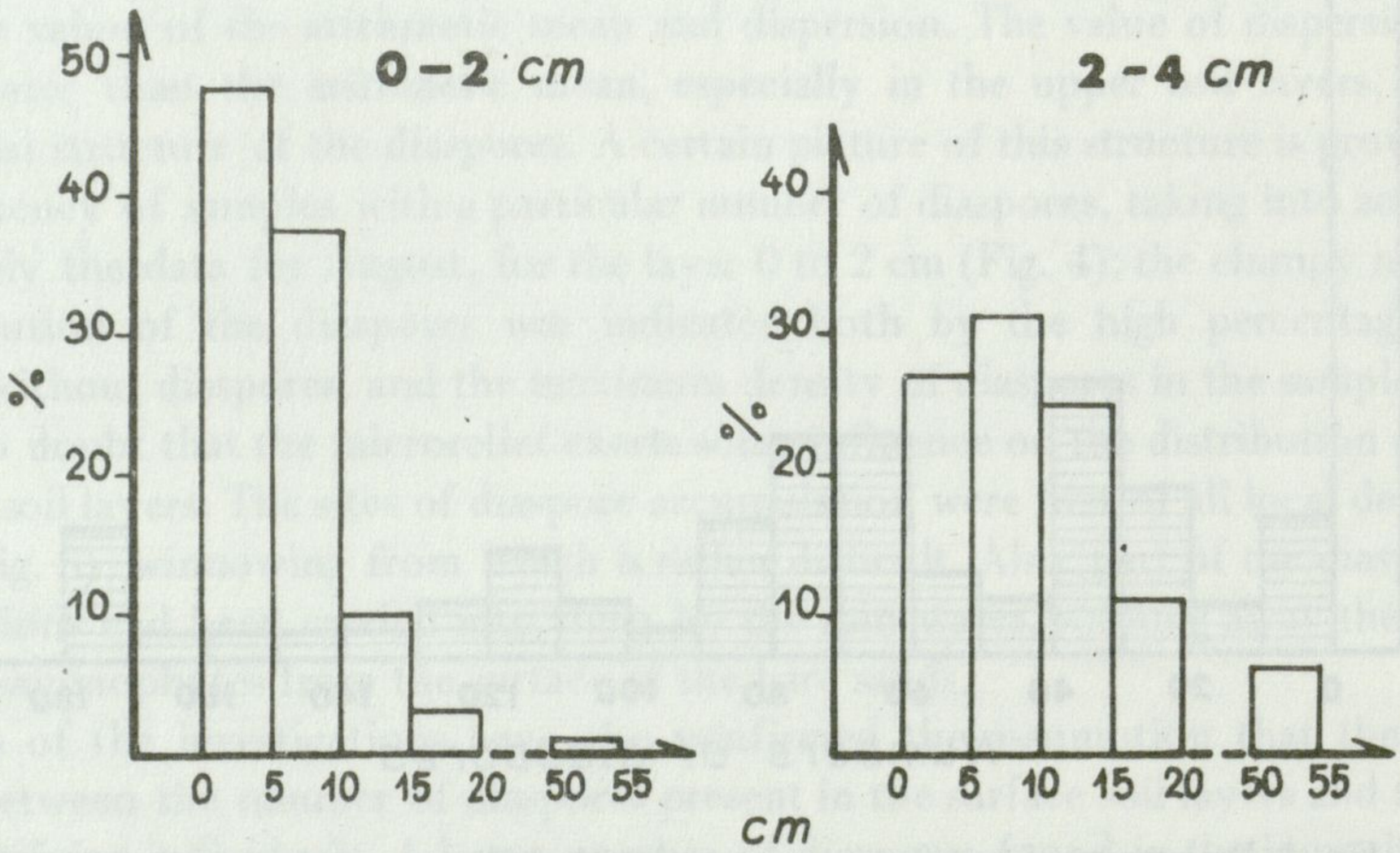

Fig. 7. Per cent of *Spergula vernalis* seeds in the surface soil layers (0–2 cm and 2–4 cm) in relation to the distance from dying individuals

seeds will first of all accumulate around the mother plant (Wilkoń-Michalska 1976), but it also indicates that the winnowing of seeds from places covered by vegetation is made difficult.

The analysis, made to complete the basic studies, of the germinating capacity of the seeds, selected from the soil, of the species that dominated in the diaspore composition indicates considerable differences between the species (Table III). A very low germinating capacity of seeds was recorded for *Festuca psammophila*, *Koeleria glauca* and *Helichrysum arenarium*. They are at the same time species which reproduce almost exclusively vegetatively, although in the surface sand layer there is a fairly large number of diaspores, from 138 to 188 per 1 m^2. Thus a lack or a small number of seedlings of the above-named species in the Spergulo-Corynephoretum patch are connected primarily with a low production of seeds capable of germinating, and not with an insufficient number of diaspores in the soils of the community. The low germinating capacity of these psammophytes is compensated for by their ability to reproduce vegetatively.

Table III. Germinating capacity of seeds of selected species

Species	Germinating (in per cent)
Corynephorus canescens	65.2
Spergula vernalis	42.5
Tragopogon heterospermus	87.5
Koeleria glauca	9.3
Festuca psammophila	7.6
Helichrysum arenarium	6.2

As expected, the per cent germination of the remainder of species was much higher (Table III), because each year a mass occurrence of their seedlings could be observed (Symonides 1977).

4. CONCLUSIONS

The results of the study suggest the following conclusions:

1. One of the causes of the clumped structure of the distribution of the seedlings of the psammophyte species is the uneven, clumped distribution of diaspores in the surface layers of the soil.

2. Accumulation of a large number of diaspores in the immediate vicinity of the individuals that produce them explains the formation of one-species aggregations of individuals, characteristic of the psammophytes, whereas the winnowing of diaspores from bare sands is responsible for the loose, masaic-like structure of the dune vegetation.

3. The high distribution of diaspore density per unit area, especially in the surface soil layers, justifies the collecting of more than 100 samples for analyses, particularly in the case of loose communities with a mosaic-like structure of vegetation, and in the case of communities situated on an open ground.

4. The over four times richer specific composition of the diaspores in the soil, relative to the specific composition of the vegetation in the community under study, indicates on the one hand a considerable ease with which foreign diaspores can penetrate the dune sands, and on the other hand the unfavourable conditions of germination and survival of seedlings in the dry and infertile habitats. However, the same data indicate that there is a possibility of succession and enrichment of the specific composition of the community with an advancing fixation of the sands and their enrichment in humus, and thus with an improvement in the water relations.

5. Because diaspores can easily be washed into the deeper layers of the porous dune soils, where they in fact lose the opportunity to germinate, and because there takes place an intense winnowing of diaspores out of the sand surface, plants whose seeds require a short rest period and are characterized by a high germinating capacity and power are more likely to successfully colonize dune habitats than are plants which produce long rest period seeds with a poor germinating capacity.

5. SUMMARY

The paper contains the results of studies on the numbers, specific composition and distribution of diaspores in the soils (dune sands) of the association Spergulo-Corynephoretum. The aim of the investigations was a trial to answer the following two questions which arose during the observations of the mortality of seedlings in psammophyte populations (Symonides 1977): (1) Do the specific composition and quantitative relations between the seedlings of the individual species in dune plant associations reflect the composition and numbers of the diaspores contained in the soil? and (2) Is the clumped spatial structure of the seedlings, characteristic of most dune species, connected with the same type of spatial distribution of the seeds in the surface soil layers?

The results of the studies are as follows:

1. The specific composition of diaspores in the soil was more than four times richer than the composition of the vegetation of the community investigated, foreign species being, however, represented by an insignificant number of diaspores (Table I, Figs. 1, 2). These results indicate on the one hand that it is possibile that foreign species can penetrate, and on the other that there are unfavourable conditions for the germinating and survival of seedlings in infertile and dry dune habitats.

2. The fairly small number of diaspores found in the soils of the community studied (Table II), although their production by most psammophytes is known to be high, resulted primarily from an intensive winnowing of diaspores from sand areas, poorly covered by vegetation, situated on an open ground.

3. During the growing season, both the total number of diaspores and the quantitative relations between the diaspores of the individual species in the surface soil layers varied considerably, depending on the time of diaspore dissemination and the time of germination (Tables I, II, Figs. 1, 2).

4. The vertical distribution of the diaspores (Fig. 3) shows that they accumulated mainly in the surface soil layers; below the level of 14 cm only single diaspores were found.

5. The horizontal spatial distribution of diaspores was of a clearly clumped nature; the percentage of "null" samples, i.e., samples without diaspores, was high, and there was a considerable percentage of samples with a large number of diaspores present (Fig. 4).

6. The largest accumulations of diaspores were found in local depressions in the ground (Fig. 5), and in the immediate vicinity of the mature individuals that produced them (Figs. 6, 7).

7. An analysis, made to complete the basic studies, of the germination of the seeds selected from the material obtained from the surface soil layers indicates that the absence of the seedlings of certain species, or their small number, result not only from the lack of a sufficient number of diaspores in the soil, but first of all from a low germinating capacity of the seeds (Table III).

6. POLISH SUMMARY

Praca zawiera wyniki badań nad liczebnością, składem gatunkowym oraz rozmieszczeniem diaspor w glebach (piaskach wydmowych) zespołu *Spergulo-Corynephoretum.* Celem tych badań była próba odpowiedzi na dwa pytania, które wyłoniły się w trakcie prowadzenia obserwacji nad wymieraniem siewek w populacjach psammofitów (S y m o n i d e s 1977): 1) czy skład gatunkowy oraz stosunki ilościowe między siewkami poszczególnych gatunków w zespołach roślinności wydmowej są odzwierciedleniem składu i liczebności diaspor zawartych w glebie? oraz 2) czy skupiskowa struktura przestrzenna siewek, charakterystyczna dla większości gatunków wydmowych, jest związana z takim samym typem rozkładu przestrzennego nasion w powierzchniowych warstwach gleby?

Oto wyniki przeprowadzonych badań:

1. Skład gatunkowy diaspor w glebie jest ponad czterokrotnie bogatszy niż skład roślinności badanego zbiorowiska, gatunki obce reprezentowane są jednak w znikomej liczbie (tab. I, rys. 1, 2). Wyniki te świadczą z jednej strony o możliwości wnikania obcych gatunków, z drugiej zaś o niekorzystnych warunkach kiełkowania i przeżywania siewek w jałowych i suchych siedliskach wydmowych.
2. Stosunkowo niska liczba diaspor występujących w glebach badanego zbiorowiska (tab. II), mimo wysokiej produkcji u większości gatunków psammofilnych, wynika przede wszystkim z intensywnego wywiewania diaspor z powierzchni skąpo pokrytych roślinnością piasków na otwartej przestrzeni.
3. Zarówno ogólna liczebność diaspor, jak też stosunki ilościowe między diasporami poszczególnych gatunków w powierzchniowych warstwach gleby zmieniają się dość znacznie w sezonie wegetacyjnym, zależnie od terminu rozsiewania diaspor i terminu kiełkowania (tab. I, II, rys. 1, 2).
4. Rozmieszczenie pionowe diaspor (rys. 3) świadczy o gromadzeniu się ich przede wszystkim w powierzchniowych warstwach gleby; poniżej 14 cm diaspory występują tylko pojedynczo.
5. Struktura przestrzenna diaspor w płaszczyźnie poziomej jest zdecydowanie skupiskowa; stwierdzono duży procent prób „zerowych", tj. bez wystąpienia diaspor oraz znaczny procent próbek z wystąpieniem dużej liczby diaspor (rys. 4).
6. Największa liczba diaspor skupia się w lokalnych zagłębieniach terenu (rys. 5) oraz w bliskim sąsiedztwie produkujących je osobników dorosłych (rys. 6, 7).
7. Przeprowadzona, w uzupełnieniu zasadniczych badań, analiza kiełkowania nasion wyselekcjonowanych z powierzchniowych warstw gleby wskazuje, że brak siewek pewnych gatunków, lub niewielka ich liczba, wynikają nie tylko z braku odpowiedniej liczby diaspor w glebie, ale przede wszystkim z niskiej zdolności kiełkowania nasion (tab. III).

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