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POPULATIONS OF *SPERGULA VERNALIS* WILLD.
ON DUNES IN THE TORUŃ BASIN

ABSTRACT: The study is concerned with the group properties of five populations of *Spergula vernalis* Willd. in relation to abiotic and biotic habitat conditions. Measurements of density included frequency, numbers and biomass, taking into account the participation of the different plant organs in biomass. The distribution of individuals in space was estimated and the results supplemented by examination of the degree of their aggregation. The natality of the populations was described on the basis of several factors: flowering and fruiting biology, pollen and seed germination capacity, fruit and seed production, weight and caloric value of seeds. Curves of survivorship were given for the populations, plotted on the basis of the number of individuals dying in several stages of ontogenesis and the net growth index of the populations.

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1. INTRODUCTION

Spergula vernalis Willd. forms an interesting object for studies, as being a pioneer plant, capable to growing in extreme biotopes poor in water and nutrient components, it constitutes an important component of primitive dune communities and is therefore the first link of succession in the process of perpetuating and covering the dunes. It also merits attention as a species reaching the eastern limit of its compact range in Poland. In addition it is valuable for several other reasons which facilitate the undertaking of ecological studies: a short life cycle, numerous occurrence in aggregations and easily obtained seeds, which it produces in abundance.

The present paper is the first in a cycle of studies on the ecology and variations of *Spergula vernalis*. On account of the great number of questions dealt with methods and results have been discussed separately in successive detailed sections of the paper.

The studies were made on five localities, each of which represented a separate stage of plant growth over the dunes. The areas varied both in respect of the composition of the flora and also the slightly different system of edaphic and microclimatic conditions, and on this account all individuals of *Spergula vernalis* from one stand have been treated in this paper as a separate population.

2. STUDY AREA

2.1. Situation, geomorphology, soils

A small part of the area (80 ha) situated to the south-west of Toruń was chosen as the site of studies and observations (Fig. 1). It lies in the foreland of a large classic complex of dunes, the relative elevations of which is as much as 20 m in places. It is located mainly within terrace VI, and only partially encroaches on to the brink of terrace IX, which is

destroyed by deflation processes, of the preglacial stream of the Vistula, which in its entirety consists of sandy formations (Niewiarowski and Tomczak 1969).

From the morphological aspect the area consists of a system of elevations usually

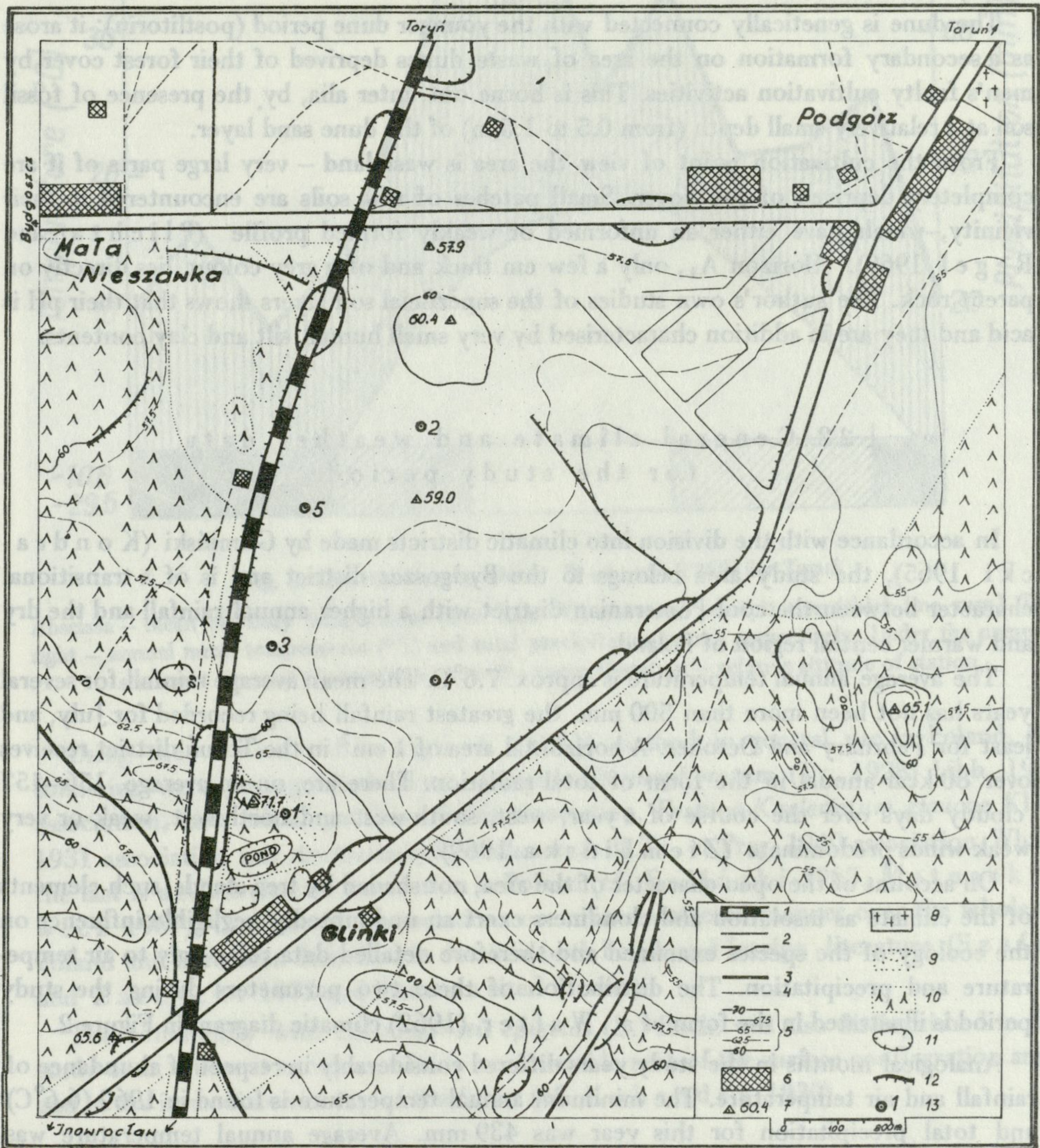


Fig. 1. Plan of study area

1 – railway, 2 – paved roads, 3 – unpaved roads, 4 – paths, 5 – isophyses, 6 – buildings, 7 – elevations, 8 – cemetery, 9 – windborne sands, 10 – forest, 11 – clay pits, 12 – slopes, 13 – selected stands

covered by windborne sands, and depressions which are in fact bombholes remaining from the Second World War. The flat parts of the area between them are thinly covered by sandloving plants.

According to Mrózek (1958) the dunes of the Toruń Basin are formed of re-winnowed terrace sands of local origin, in which fine earth predominates. The first level of subsoil water is situated at a depth of 5–6 m (Mrózek and Regel 1965).

The dune is genetically connected with the younger dune period (postlitorin): it arose as a secondary formation on the area of waste dunes deprived of their forest cover by man's faulty cultivation activities. This is borne out, inter alia, by the presence of fossil soil at a relatively small depth (from 0.5 to 1.5 m) of the dune sand layer.

From the cultivation point of view the area is wasteland – very large parts of it are completely deprived of soil cover. Small patches of raw soils are encountered in their vicinity, which have either an unformed or weakly formed profile (Plichta and Regel 1969). Horizon A₁, only a few cm thick and of a grey colour, lies directly on parent rock. The author's own studies of the superficial soil layers shows that their pH is acid and they are in addition characterised by very small humus, silt and clay contents.

2.2. General climate and weather data for the study period

In accordance with the division into climatic districts made by Gumiński (Kondracki 1965), the study area belongs to the Bydgoszcz district and is of a transitional character between the cool Pomeranian district with a higher annual rainfall and the dry and warmer central region of Poland.

The average annual temperature is approx. 7.6°C. The mean average rainfall for several years has not been more than 500 mm, the greatest rainfall being recorded for July, and least for February and October. A horizontal area of 1 cm² in the Toruń district receives over 80 kcal annual in the form of total radiation. There are, on an average, 156–157 cloudy days over the course of a year, west, south-west and northwest, weak or very weak winds predominate (Ziembińska 1969).

On account of the open character of the area, not shaded by tree stands, such elements of the climate as insolation and cloudiness exert an undoubtedly negligible influence on the ecology of the species examined and therefore detailed data refer only to air temperature and precipitation. The distribution of these two parameters during the study period is illustrated in the form of a Walter (1962) climatic diagram in Figure 2.

Analogical months in the study years differed considerably in respect of abundance of rainfall and air temperature. The minimum annual temperature is found in 1969 (6.6°C) and total precipitation for this year was 439 mm. Average annual temperature was highest in 1968 (7.9°C), and total precipitation highest in 1970 (738 mm).

2.3. Description of vegetation

Despite the unfavourable conditions for vegetation formed by the soil sand, poor in nutrient components and silt and clay, the flora of the study area is fairly varied. Over 100 species of plants occur there, 90 of which are flowering plants and less than twenty mosses and lichens.

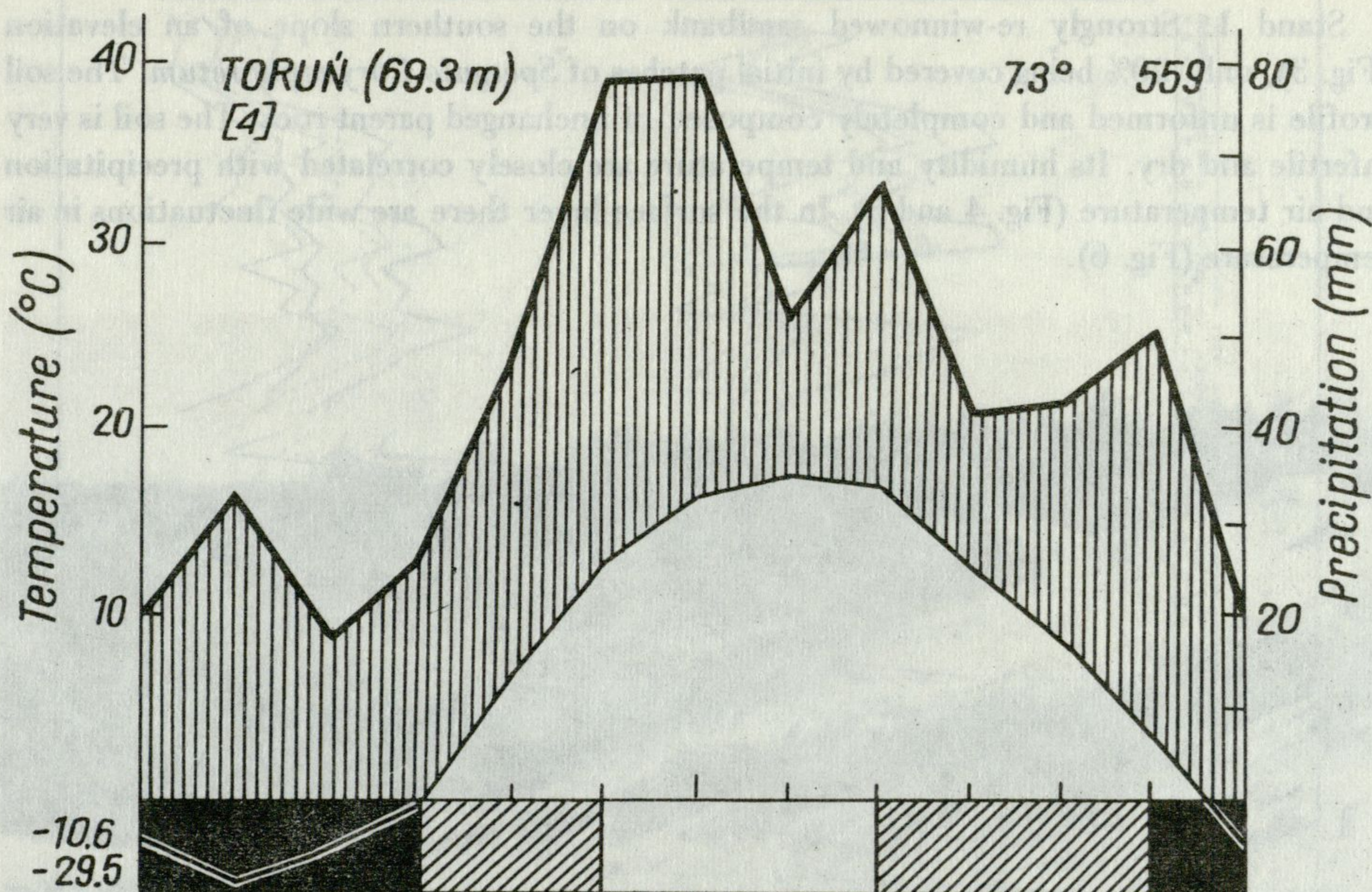


Fig. 2. Climatic diagram (after Walter 1962) for Toruń

Abscissa – mean monthly temperature (thin line, °C) and total precipitation (thick line, mm). Top right – annual mean temperature (°C) and total precipitation (mm), respectively. Under the name of station – years of observations. Near the name of station – relative altitude of station

Using the Braun-Blanquet (1951) method in general use in Poland, the following were distinguished there: *Spergulo-Corynephorum* (Tx. 1928) Libb. 1933 association, also initial patches of this association, *Festuco-Koelerietum glaucae* Klika 1931 association and *Arctostaphyllo-Callunetum* R. Tx. et Prag. 1940 association. While the last is a relatively rare association in Poland (cf. Faliński 1965, Matuszkie-wicz 1967), the first two associations occur in a scattered manner over the whole of Poland and have been described in detail in both Polish and foreign literature (Szafer and Zarzycki 1972 and literature cited therein).

The community with *Calamagrostis epigeios* (L.) Roth. was also distinguished in the study area, where it occupies a fairly considerable part of the surface conflagration areas and in the immediate vicinity of the forest (cf. Kobendza 1930).

2.4. Description of stands

As indicated in the introduction, the areas chosen for the study differed in respect of the permanency and degree of plant cover on the sands, the composition and abundance of species and in consequence – the physical and chemical properties of the soils.

Stand 1. Strongly re-winnowed sandbank on the southern slope of an elevation (Fig. 3), only 20% being covered by initial patches of *Spergulo-Corynephorum*. The soil profile is unformed and completely composed of unchanged parent rock. The soil is very infertile and dry. Its humidity and temperature are closely correlated with precipitation and air temperature (Fig. 4 and 5). In the surface layer there are wide fluctuations in air temperature (Fig. 6).



Fig. 3. Stand 1

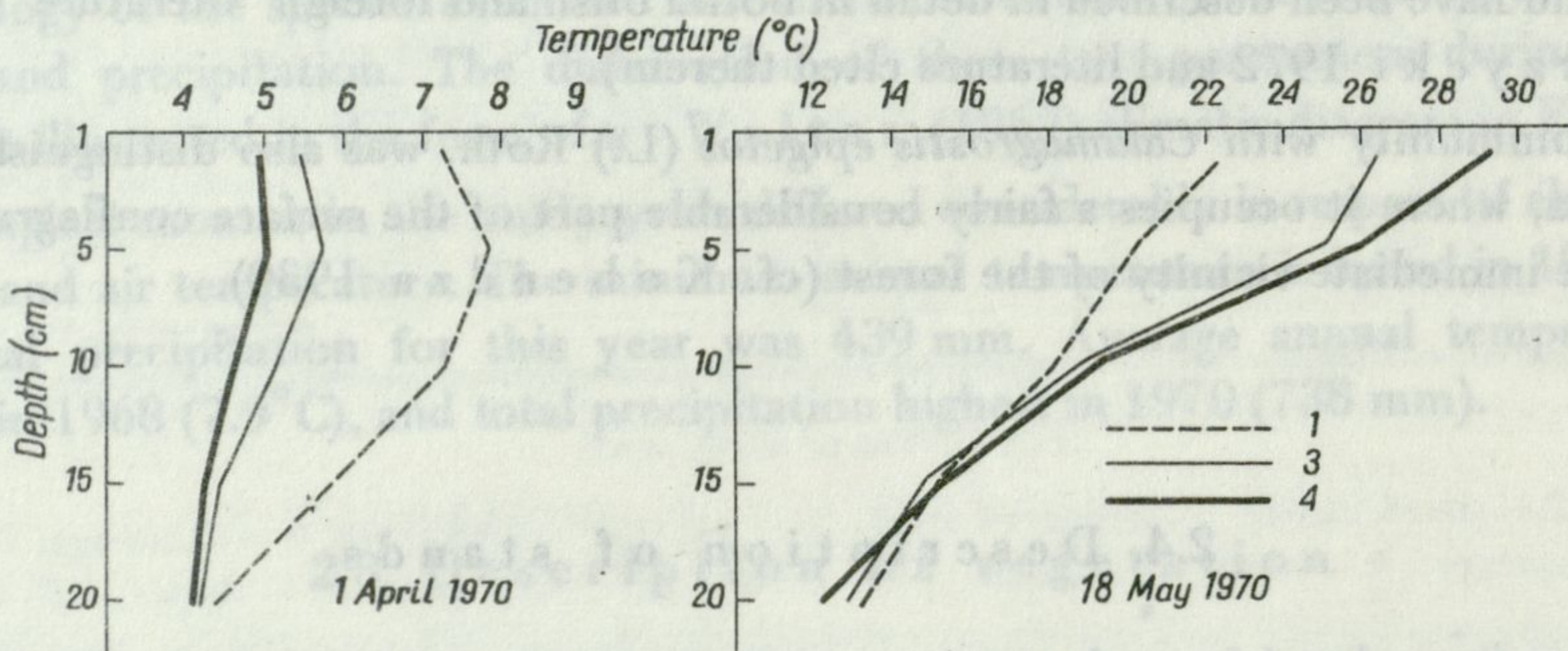


Fig. 4. Comparison of soil temperature on stands 1, 3 and 4 with air temperature 9.7°C (left side) and 30.7°C (right side)

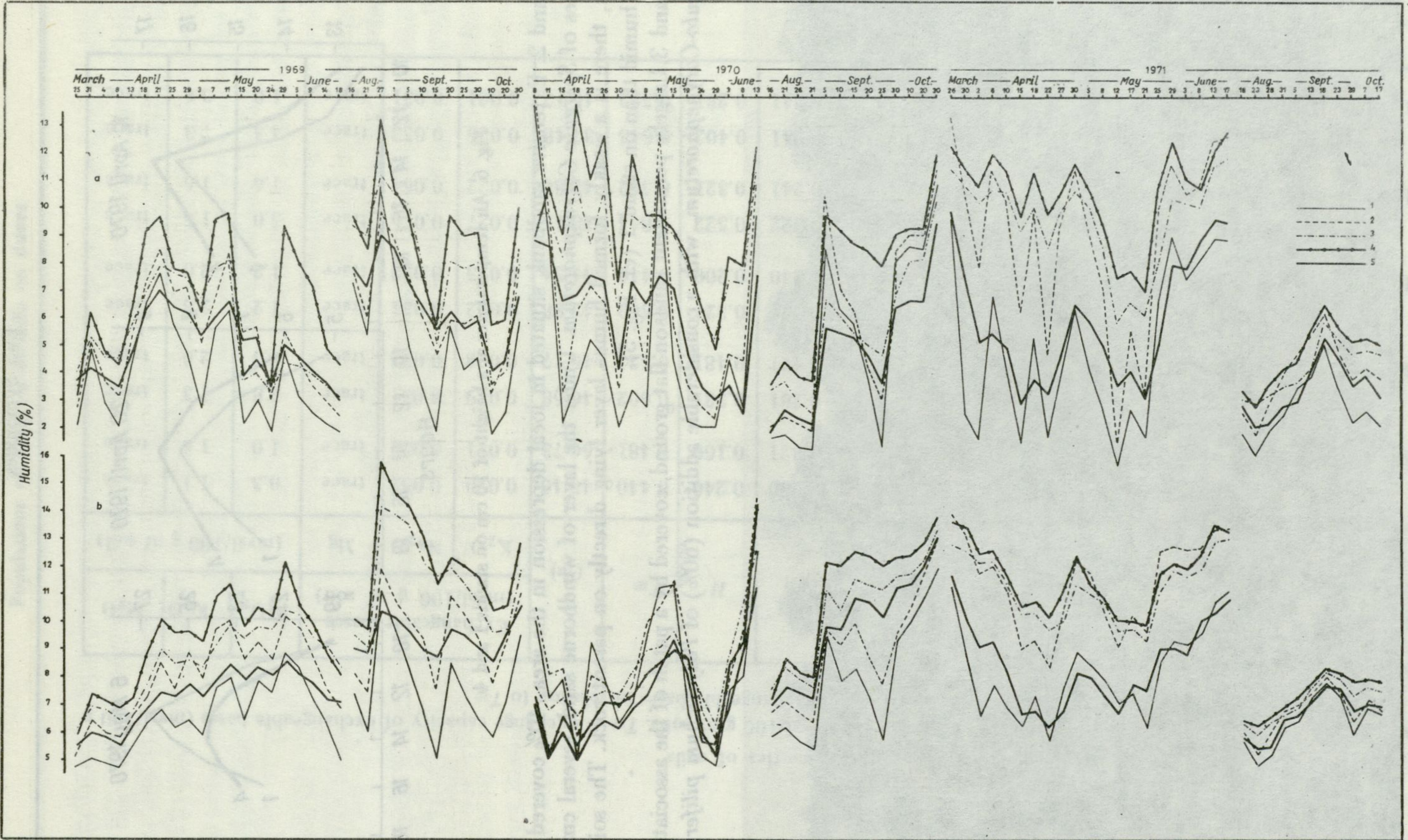


Fig. 5. Dynamics of soil moisture on five stands in 1969-1971

a - depth 2-7 cm, b - depth 15-20 cm

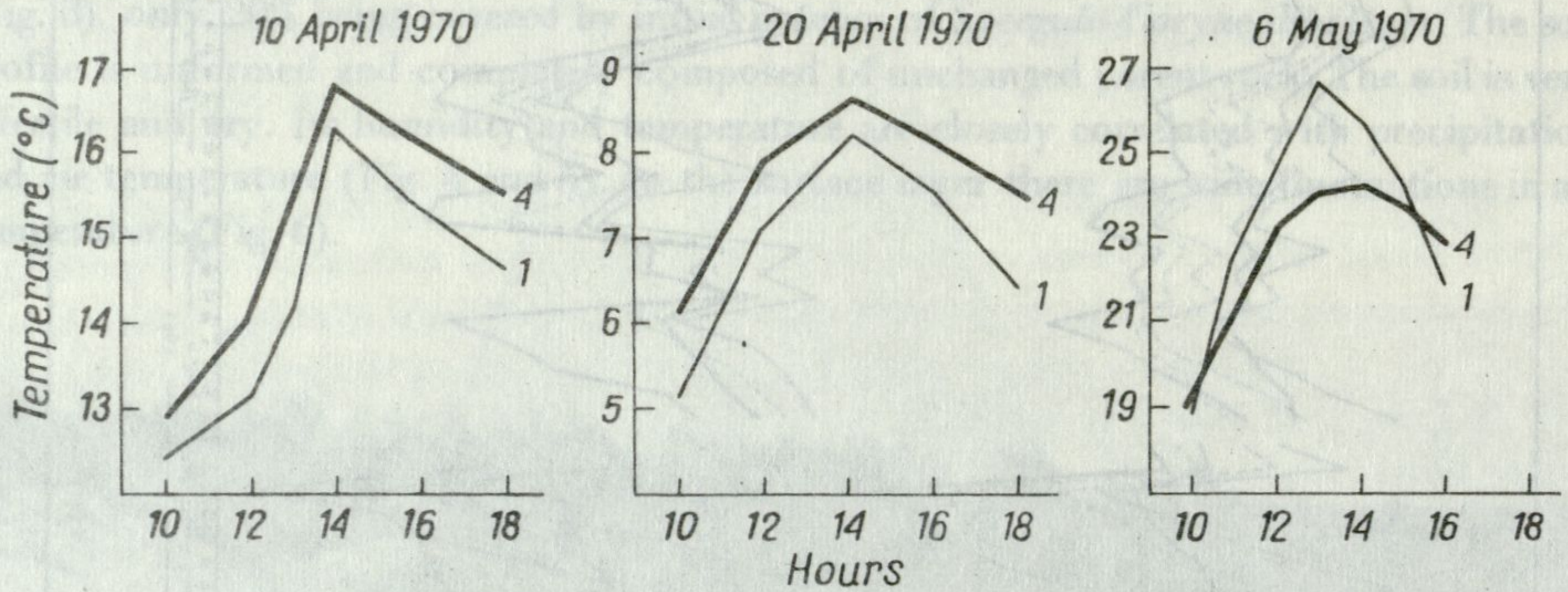


Fig. 6. Air temperatures at a height of 10 cm on stands 1 and 4

Stand 2. Extensive sandbank situated in local depression in the area, 40% covered by patches of *Spergulo-Corynephorum*. Under the layer of windborne sand, several cm in depth, there is a weakly formed humus layer lying directly on parent rock. The soil is more humid than on stand 1 (cf. Fig. 5).

Stand 3. Largely permanent sandson flat ground, covered by a patch of the association *Spergulo-Corynephorum*, with a considerable addition (60%) of *Polytrichum piliferum*



Fig. 7. Stand 4

Tab. I. Chemical properties of soils

S – total exchangeable basis (mval/100 g of soil), *H* – exchange acidity (mval/100 g of soil), *T_w* – exchange capacity of exchangeable bases (mval/100 g of soil), *V* – degree of saturation of soil with exchangeable bases in relation to *T_w*

Stand	Depth of sampling (cm)	pH (KCl)	Ash (%)	CaCO ₃ (%)	Humus (%)	Hydrolytic acidity of soil (mval/100 g of soil)	<i>S</i>	<i>H</i>	<i>T_w</i>	<i>V</i> (%)	Exchangeable bases (mval/100 g of soil)			P ₂ O ₅	K ₂ O	MgO
											K ₂ O	Na ₂ O	Mg			
1	2-7	4.4	99.61	0.0	0.23	1.66	0.200	0.240	0.440	45.45	0.020	0.052	trace	0.3	1.1	trace
	12-17	4.8	99.66	0.0	0.25	1.55	0.321	0.160	0.481	66.73	0.021	0.053	trace	1.0	1.6	trace
2	2-7	4.3	99.24	0.0	0.53	2.34	0.281	0.321	0.602	46.68	0.019	0.051	trace	2.8	1.3	trace
	12-17	4.8	98.63	0.0	0.93	3.17	0.241	0.481	0.522	46.17	0.022	0.055	trace	4.3	2.0	trace
3	2-7	4.8	99.28	0.0	0.38	1.89	0.241	0.321	0.562	42.88	0.022	0.051	trace	1.2	2.5	trace
	12-17	5.0	99.69	0.0	0.17	1.43	0.240	0.200	0.440	54.54	0.015	0.038	trace	1.2	2.0	trace
4	2-7	3.8	96.79	0.0	1.40	4.30	0.322	0.522	0.844	38.15	0.027	0.076	trace	5.0	1.5	trace
	12-17	4.4	99.44	0.0	0.42	2.34	0.241	0.321	0.562	42.88	0.022	0.064	trace	1.6	1.6	trace
5	2-7	4.2	98.62	0.0	1.10	2.87	0.241	0.402	0.643	37.48	0.026	0.053	trace	4.3	7.3	trace
	12-17	4.5	99.61	0.0	0.21	1.81	0.241	0.281	0.522	46.17	0.021	0.051	trace	1.0	3.6	trace

Schreb. The soil profile is weakly formed. The humus layer (3 cm) lies on parent rock. There are lesser fluctuations in temperature and humidity than on stand 1 (Fig. 4 and 5).

Stand 4. Extensive moor (Fig. 7) on flat land (*Arctostaphylo-Callunetum*) with considerable percentage of *Cladonia rangiferina* (L.) Web. (75%). Distinct humus layer (6 cm) in the soil profile lying on slightly changed parent rock. Soil contains more water and nutrient components than on stands 1, 2, 3 (Tab. I, Fig. 5). The compact shrub vegetation results in a milder air temperature in the layer above ground level (Fig. 6).

Stand 5. The most advanced stage of plant cover of the dune in this area. The dominating species here is *Calamagrostis epigeios*. The soil profile is similarly formed to that on stand 4. Soil dry but relatively rich in nutrient components (Tab. I, Fig. 5).

On account of the initial character of soils and the shallow root system of *Spergula vernalis*, soil analysis was limited only to the superficial layer (2–7 cm and 12–17 cm). The results, set out in Figure 8 (physical properties) and in Table I (chemical properties),

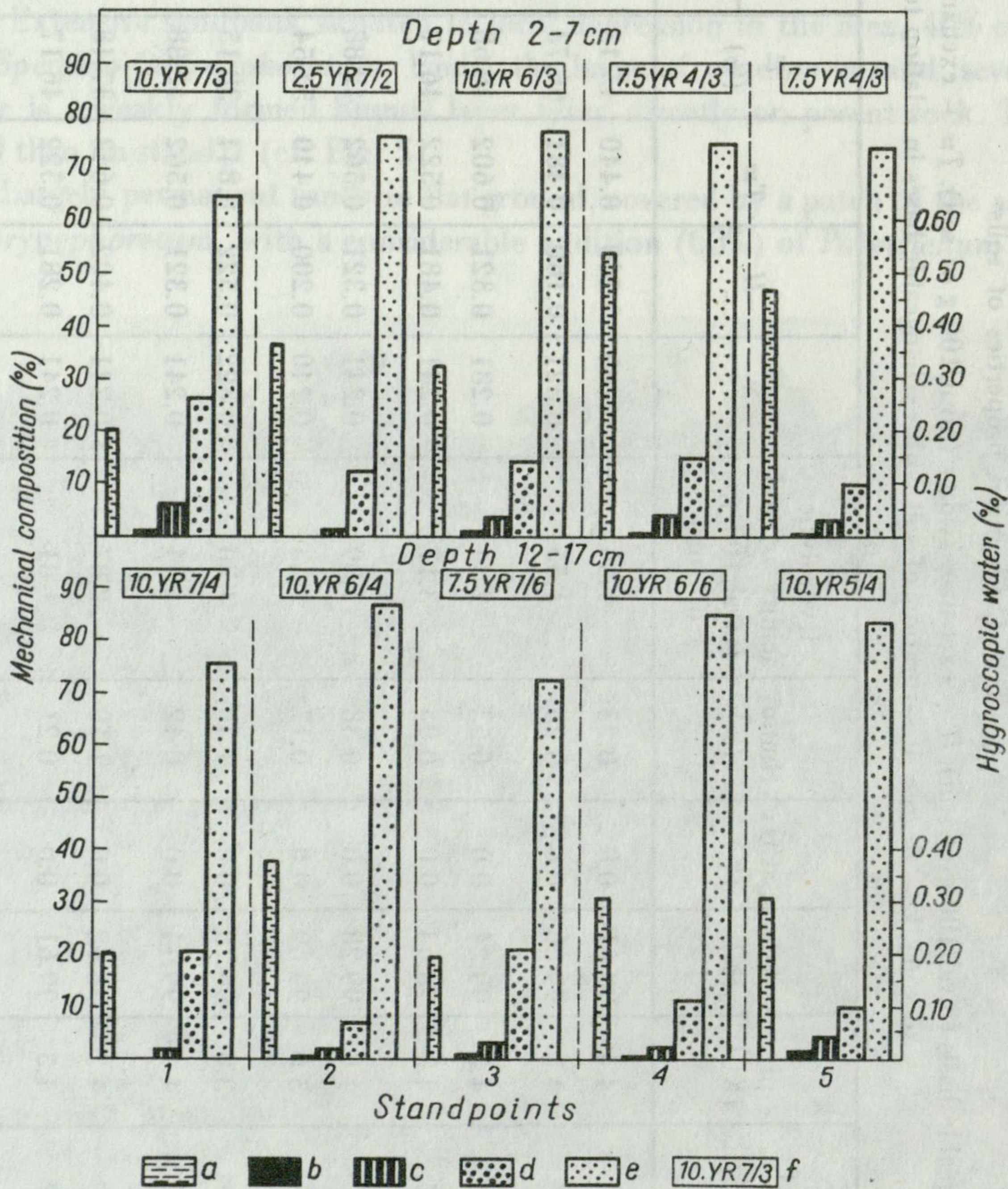


Fig. 8. Physical properties of soils

a – hygroscopic water, b – skeletal particles (diameter > 1 mm), c – coarse sand (diameter 1.0–0.5 mm), d – medium sand (diameter 0.5–0.25 mm), e – fine sand (diameter 0.25–0.10 mm), f – soil colour (after Standard Soil Colour Chart)

show that soils from the selected stands are formed from loose, lime-free sands, in which the fine earth predominates: they are acid and very poor in nutrient components (P, K, Mg). Hygroscopic moisture does not usually exceed 0.5%. Differences between stands are chiefly in respect of humus content, which in turn affects the other properties of the soils.

Examination was also made of the soil moisture dynamics of five stands during the growing season of *Spergula vernalis*. Soil moisture was determined by drying soil samples at a temperature of 105°C. The percentage of water held by the soil on a dry basis is the moisture content (K o w a l i ń s k i et al. 1969). The course taken by moisture curves for 1969–1971 at depths of 2–7 cm and 15–20 cm is illustrated by Figure 5. Data show that: (a) particularly striking differences in moisture in successive measurements are found on stands with scanty plant cover (1 and 2); such differences are far smaller on stands with dense plant cover (3, 4 and 5); (b) apart from a few exceptions soil moisture is greatest on stand 4, and very low on stand 1; (c) differences between stands, most distinct during periods of lengthy droughts, are primarily due to differences in plant cover, which effectively protects the superficial layers of the soil from excessive drying.

3. GROUP PROPERTIES OF POPULATIONS OF *SPERGULA VERNALIS*

3.1. Scope of studies

The population is characterized by a large number of group properties which neither individuals nor the biocenosis possess nor compose. Among the more important of those, which have been taken into consideration in this study, are: (a) density, or the population numbers per unit of area, (b) spatial structure – way in which individuals are distributed in space, (c) natality – rate at which new individuals are added to population by reproduction, (d) mortality – rate at which individuals disappear from the population as the result of their death, (e) index of net population growth – the final result of natality and mortality.

Studies of the group characters of the population were made from 1969 to 1971. Each population was given the same number as that of the stand from which it originates.

3.2. Density and spatial distribution

3.2.1. Premises and methods

Measurements of density in population studies are as a rule made in order to estimate the influence exerted by a population on biocenosis and ecosystem (O d u m 1963), to define reciprocal relations between individuals (P o n y a t o v s k a y a 1964) and obtain a good exponential of the ecological conditions in the habitat of the species examined (T r a c z y k 1967), on the basis of which the ecological optimum of the population can be determined (R a b o t n o v 1945, S m i r n o v a 1968).

Density is usually expressed either in the number of individuals or their biomass per unit of area. The first way is satisfactory when the size of individuals in a population is relatively balanced, otherwise it is better to estimate density on the basis of biomass (O d u m 1963). If the distribution of individuals in space is irregular use should in addition be made of dispersion index. In relation to plant populations the index of dispersion and density in common use is the frequency, that is the percentage of test areas in which at least one example occurs.

The choice of size and number of samples in measurements of density is of primary importance and depends in the first place on the object studied. The shape of the test area is also of some importance, as shown by the experiments made by D y n e, V o g e l and F i s s e r (1963): samples taken from circular areas give more satisfactory results than those from rectangular ones, as they reduce variance.

On account of the uneven distribution in space of individuals of *Spergula vernalis*, the presence of branching, in addition to unbranching, forms, the latter being obviously characterized by lesser biomass and considerable difference in size of individuals within one population, all the above methods were used in the density analysis.

Measurements were made in 1970 and 1971 during the fruiting period of *Spergula vernalis*, which permitted not only of estimating maximum biomass (corresponding in the case of annual plants to their production) but also fruit production.

Frequency was determined on each stand from one hundred random casts of a hoop 0.1 m² in area (diameter 36.7 cm), after which the number of casts was increased in order to obtain one hundred "full" casts, that is, with the species occurring in the sample. Each sample was analyzed in respect of the number of branching and non-branching individuals (in order to establish the percentage of participation of the former) and their biomass. The plants were dug up whole, segregated into roots, stems and fruits, and weighed with accuracy to 0.001 g after drying for 48 hours at 85°C.

Density was analyzed in a similar way in permanent squares 10 m² in area, divided into one hundred smaller units, the area of the unit squares corresponding to the area of random samples. The squares were marked out on each stand in the place best reflecting the character of the biotope: they then formed the "representative model" of each population (S o c h a v a, L i p a t o v a and G o r s h k o v a 1962).

The weight of an average individual in a sample was calculated from biomass value and numbers and also the participation in percentages of the various organs in the whole biomass.

In addition calculation was made of the coefficients of correlation in order to find the correlation between numbers and weight of an individual in a sample.

The question of population density is connected with the type of distribution of individuals in space and the degree to which they clumped. When individuals are unevenly distributed in space average density does not form a true measure of their aggregation in a unit of area (M a c A r t h u r and C o n n e l l 1971). It is then better to use the term of so-called "mean crowding" defining the number of other individuals constantly present in the same unit of area per one individual [Lloyd 1966; cited after M a c A r t h u r and C o n n e l l (1971)]. Average crowding is a very adequate exponential of the actual interpopulation dispersion.

Among the large number of methods for defining the spatial distribution of populations two are most often used. The first of these, proposed by Dice, consists in measuring in

a certain standard way the distance between individuals (Pielou 1960, 1961, 1962, Vasilevich 1969); the second, which has been used in the present study, consists in comparing the actual frequencies of groups of different size (numbers) with Poisson's series, which describe the frequency of analogical groups in random dispersion. Deviation from theoretical proportions of random distribution are usually checked by means of the χ^2 test (Cole 1946, Greig-Smith 1962, Perkal 1967, Whittaker 1970), although Vasilevich (1969) proposes a large number of other equations.

The spatial structure of the populations examined was analyzed on permanent squares measuring 10 m², divided into one hundred unit squares. "Mean crowding" was calculated for these areas on the basis of Lloyd's equation (MacArthur and Connell 1971) and the ratio of "mean crowding" to mean density, which according to Lloyd forms a good index of the dismemberment of the habitat.

3.2.2. Discussion of results

One remark must be made as incidental to the discussion of results. In ecology a difference is made between the concept of "total density" per unit of the whole area, not infrequently as distinct from "specific" or "ecological" density (also termed "economic"), relating to a unit only of such an area as can be occupied by the population. In the given case, the second treatment made it possible to obtain a truer picture of the actual situation, particularly when frequency was simultaneously taken into consideration. Hence numbers and biomass of random samples describe only ecological density, whereas for the permanent squares values of total density were given in addition, on account of the necessity for taking "null samples" into consideration in estimating the type of spatial distribution of the population.

All data on density and spatial structure of the populations studied are set out in Tables II and III and Figure 9. They reveal fairly considerable differences, in extreme cases both in respect of degree of occupation of the area (shown by frequency) and also of numbers and production of mass. High average value and maximum density are characteristic of populations 2 and 4, very low of populations 1 and 5; population 3 occupies a place intermediate between these. It must be emphasised that with the exception of biomass of populations 2 and 4, statistically significant differences were found.

The distribution of individuals in space within each population can be considered as the clumped type (probability that distribution is random $p < 0.001$). This is shown by values of χ^2 and of "mean clumping" (Tab. III), far exceeding not only total density but in general also ecological density. The ratio of mean clumping to mean density is the higher, the smaller frequency and average numbers of the population. A high degree of clumping is characteristic particularly of population 1, then population 5. Proceeding in the direction of further division of types of distribution, both cases may be considered as belonging to aggregated clumped patterns. Dispersions of the other populations exhibit a tendency towards the random clumped type.

Dispersion and density of plants, in Snaydon's (1962) opinion, is the function of supply and distribution in the soil of nutrient components. Ponyatovskaya (1964) emphasises the importance of the properties of the biotope, but nevertheless lays particular stress on the biology and ecology of the species and the random element in the

Tab. II. Comparison of density in five populations (results obtained by the random sample method)

Population	Year	Frequency (%)	Branching individuals (%)	Numbers per 0.1 m ²		Biomass (g/0.1 m ²)		Average weight of individual (g)	Participation of organs in total biomass (%)		
				maximal	mean	maximal	mean		stems	roots	fruits
1	1970	35	33.1	22	11.2 ± 2.5	0.56	0.37 ± 0.06	0.0327 ± 0.0039	47.9 ± 1.4	10.5 ± 1.2	41.4 ± 1.7
	1971	31	39.0	19	11.3 ± 2.7	0.52	0.36 ± 0.03	0.0324 ± 0.0036	47.7 ± 1.5	9.7 ± 1.4	42.3 ± 1.2
2	1970	61	25.3	49	26.6 ± 7.2	0.91	0.63 ± 0.11	0.0241 ± 0.0024	33.6 ± 3.8	8.6 ± 2.7	57.8 ± 4.3
	1971	73	25.8	47	27.2 ± 7.1	0.71	0.61 ± 0.08	0.0242 ± 0.0027	32.4 ± 4.0	9.0 ± 2.4	58.7 ± 2.8
3	1970	74	17.5	45	19.6 ± 6.2	0.76	0.49 ± 0.12	0.0266 ± 0.0036	44.9 ± 1.6	8.8 ± 1.0	46.7 ± 1.1
	1971	71	22.6	41	19.1 ± 6.1	0.67	0.42 ± 0.10	0.0267 ± 0.0037	45.2 ± 1.1	8.8 ± 1.1	46.6 ± 1.1
4	1970	80	18.7	48	20.5 ± 7.6	1.62	0.63 ± 0.21	0.0324 ± 0.0089	45.6 ± 1.2	6.5 ± 0.8	47.6 ± 1.5
	1971	85	20.5	46	18.2 ± 6.5	1.29	0.61 ± 0.16	0.0341 ± 0.0097	46.1 ± 1.4	7.1 ± 1.1	47.3 ± 1.4
5	1970	64	11.8	17	9.3 ± 3.1	0.23	0.14 ± 0.04	0.0164 ± 0.0031	45.2 ± 1.2	8.2 ± 1.4	47.7 ± 2.6
	1971	67	13.2	20	9.2 ± 3.2	0.34	0.15 ± 0.05	0.0165 ± 0.0031	45.4 ± 1.1	8.2 ± 1.8	47.0 ± 2.5

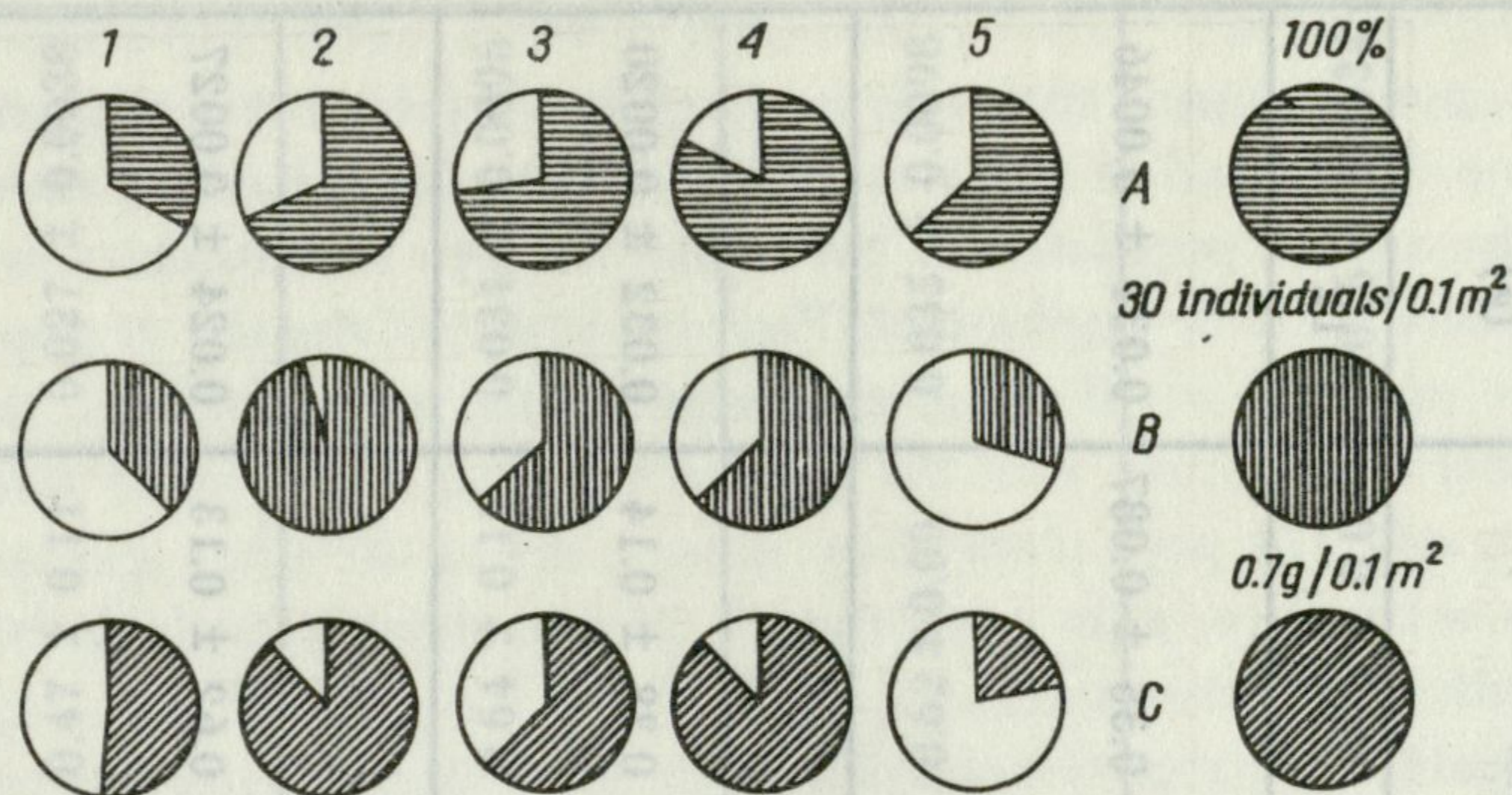


Fig. 9. Comparison of frequency (A), numbers (B) and biomass (C) in the five study populations (diagrams illustrate the mean values for two years obtained by the random sample method)

self-sowing of plants. According to Harper, Williams and Sagar (1965), the density of plants reproducing through seeds is determined to a considerable extent by the microtopography of the area and the number of "safe places for germination" connected with the local relief. In relation to dry biotopes, with the mosaic structure of vegetation typical of them, the opinion put forward by Mazing (1970), recognizing water content in soil as a dominating factor influencing density and spatial distribution of a population, deserves particular attention.

The findings of the above authors in principle cover the whole of the question, although more attention should be given to the problem of competition. The competitive power of a species is of equal importance in the process of its occupation of space as the potential possibilities created by a favourable system of physical and chemical and biological properties of a biotope.

Certain difficulty is encountered in attempting to interpret the results obtained on the basis of the premises put forward by the above researchers and the actual properties of a biotope. The degree of density is undoubtedly the resultant of the simultaneous action of a large number of factors, hence it is possible to give approximate emphasis to one of them only and in relation to one population.

The low frequency and density of population 1 would appear to be understandable in view of the extreme dryness and poverty in nutrient components of the soil. The distinct tendency of individuals to clump and the high percentage of branched forms most probably result from defensive reaction to deflation processes, which are particularly intensive on stand 1 with its scanty plant cover. Greater clumping of plants (up to a certain limit) provides better chances of survival under extreme conditions than is the case with single individuals (cf. Allee et al. 1958).

Similarly low density values were found in population 5, although in this case the limiting factor is most certainly the greater competitive power of competitors (cf. Caplenor 1964). During the four-year study period the retreat of *Spergula vernalis* from areas which it had previously occupied, with simultaneously increasingly numerous appearance of more dynamic species, such as *Calamagrostis epigeios* and *Carex ericetorum* Poll., could be traced without difficulty.

A more favourable set of conditions was found in the other populations, as is shown by the greater abundance and production of organic mass (both mean and maximum

Tab. III. Comparison of density and spatial structure in five populations (results obtained by analyses of 100 squares forming total area of 10 m²)

Population	Year	Number of individuals per 0.1 m ² (n)	Mean density (total) (M)	Number of squares with n found	Anticipated number of squares with n	χ^2	Mean crowding (m_o)	$\frac{m_o}{M}$	Number of individuals per 0.1 m ²	Biomass (g/0.1 m ²)	Average weight of individual (g)
1	2	3	4	5	6	7	8	9	10	11	12
1	1970	0 1-4 5-8 9-12 13-16 17-20	3.72	67 1 4 18 7 3	37.0 37.0 18.0 6.0 1.5 0.3	216.7	33.72	9.1	11.3 ± 3.6	0.35 ± 0.087	0.031 ± 0.0046
	1971	0 1-4 5-8 9-12 13-16 17-20	3.06	72 1 4 16 6 1	42.0 36.0 15.0 4.0 1.0 0.01	221.9	40.86	13.3	10.9 ± 2.9	0.38 ± 0.14	0.032 ± 0.0020
2	1970	0 1-10 11-20 21-30 31-40 41-50	16.90	37 0 21 27 10 5	15.0 29.0 27.0 17.0 8.0 3.0	68.7	26.40	1.5	26.8 ± 6.8	0.62 ± 0.13	0.024 ± 0.0027
	1971	0 1-10 11-20 21-30 31-40 41-50	20.80	22 2 7 50 18 1	9.0 22.0 27.0 21.0 13.0 6.0	98.8	27.00	1.3	26.7 ± 6.1	0.61 ± 0.08	0.025 ± 0.0028

3	1970	0 1-10 11-20 21-30 31-40 41-50	14.30	28 9 32 26 3 1	19.0 31.0 26.0 15.0 6.0 2.0	24.9	16.10	1.8	19.8 ± 7.4	0.48 ± 0.14	0.026 ± 0.0036
	1971	0 1-10 11-20 21-30 31-40 41-50	13.22	32 7 31 27 2 1	19.0 32.0 26.0 14.0 6.0 2.0	42.6	25.44	1.9	19.4 ± 6.7	0.47 ± 0.11	0.027 ± 0.0038
4	1970	0 1-10 11-20 21-30 31-40 41-50	16.48	19 6 39 29 6 1	14.5 27.0 27.0 18.0 9.0 4.5	33.29	24.97	1.5	20.3 ± 6.7	0.64 ± 0.16	0.034 ± 0.0096
	1971	0 1-10 11-20 21-30 31-40 41-50	16.96	14 8 40 36 1 1	13.0 26.0 27.0 19.0 10.0 4.0	45.3	23.64	1.4	19.7 ± 7.4	0.62 ± 0.09	0.035 ± 0.0098
5	1970	0 1-4 5-8 9-12 13-16 17-20	6.75	34 0 16 37 12 1	14.0 28.0 27.0 18.0 9.0 3.0	66.0	15.55	2.3	10.2 ± 2.6	0.16 ± 0.07	0.016 ± 0.0034
	1971	0 1-4 5-8 9-12 13-16 17-20	6.70	31 3 23 34 7 2	15.0 29.0 27.0 17.0 8.0 3.0	57.0	16.10	2.4	9.7 ± 3.2	0.16 ± 0.06	0.017 ± 0.0057

values) and more complete occupation of the area (higher frequency; cf. Fig. 9). On stand 3 – the compact moss turf and on stand 4 – lichen turf – protect the superficial soil layers from drying and in this way ensure a better supply of water to the plants. In addition, in the case of population 4, the higher content of nutrient components of the soils on this stand must be emphasised. The high degree of density of population 2 is due to the absence of plants of other species competing for space and food, the relatively fair supply of water (connected with the local depression in the area) and nutrient components in the soil. The poor plant cover accompanying the study species brought about the numerous occurrence, as in population 1, of branching individuals better adapted to the struggle with windborne sand.

The participation of roots, stems and fruits in total biomass is similar in all populations (Tab. II), and the high percentage of dry mass of fruits, forming about 50% (in population 2 over 50%) of the whole biomass and very low percentage formed by root mass, are also generally characteristic. Proportions of this kind are characteristic of the majority of annual plants adapted to life in open communities (Salisbury 1952, Struik 1965).

The average weight of an individual is an equally valuable indicator of the "abundance" of a population as density (Ponyatovskaya 1964); it shows the organic mass contributed by an individual in the total circulation of matter and energy of each specific plant community,

The results obtained are not fully comparable in this respect, on account of the differences in participation of branching forms. Their high percentage can be explained by the large average weight of an individual in population 1. When populations 3 and 4, similar in respect of the participation of branching individuals, are compared, the particularly great mass of the average individual in population 4 is remarkable; the lowest weight per individual was found in population 5.

The results of correlation between numbers and weight of an individual in a sample are interesting (Fig. 10, 11 and 12). In populations with relatively high density (2, 3 and 4) a significant negative relation can be found between the two parameters: with low density

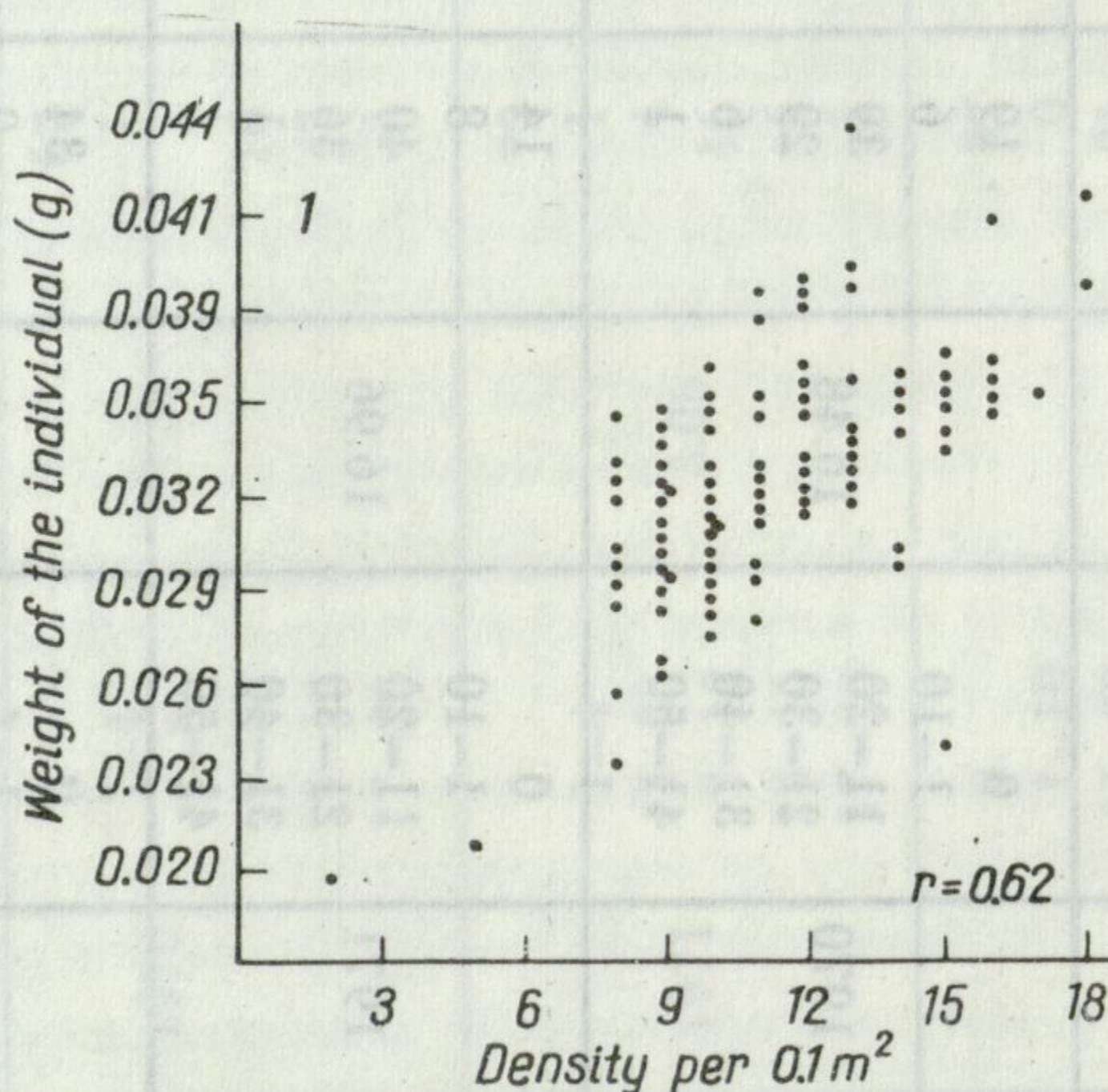


Fig. 10. Diagram of relation between weight of an individual and density (population 1)

(populations 1 and 5) coefficients of correlation are positive. The lower production of each individual above a certain degree of density is particularly strikingly obvious in poor stands (Salisbury 1942).

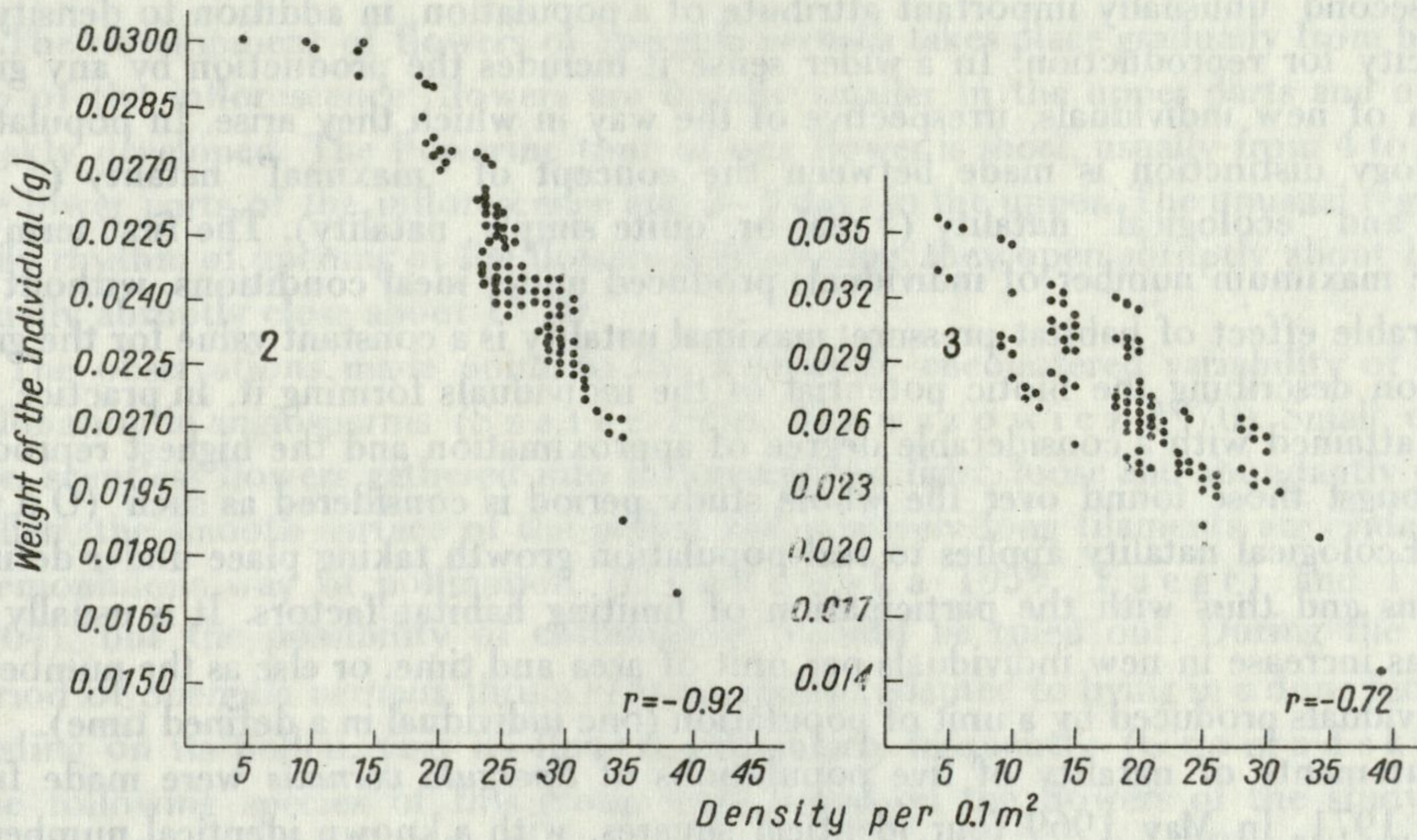


Fig. 11. Diagram of relation between weight of an individual and density (populations 2 and 3)

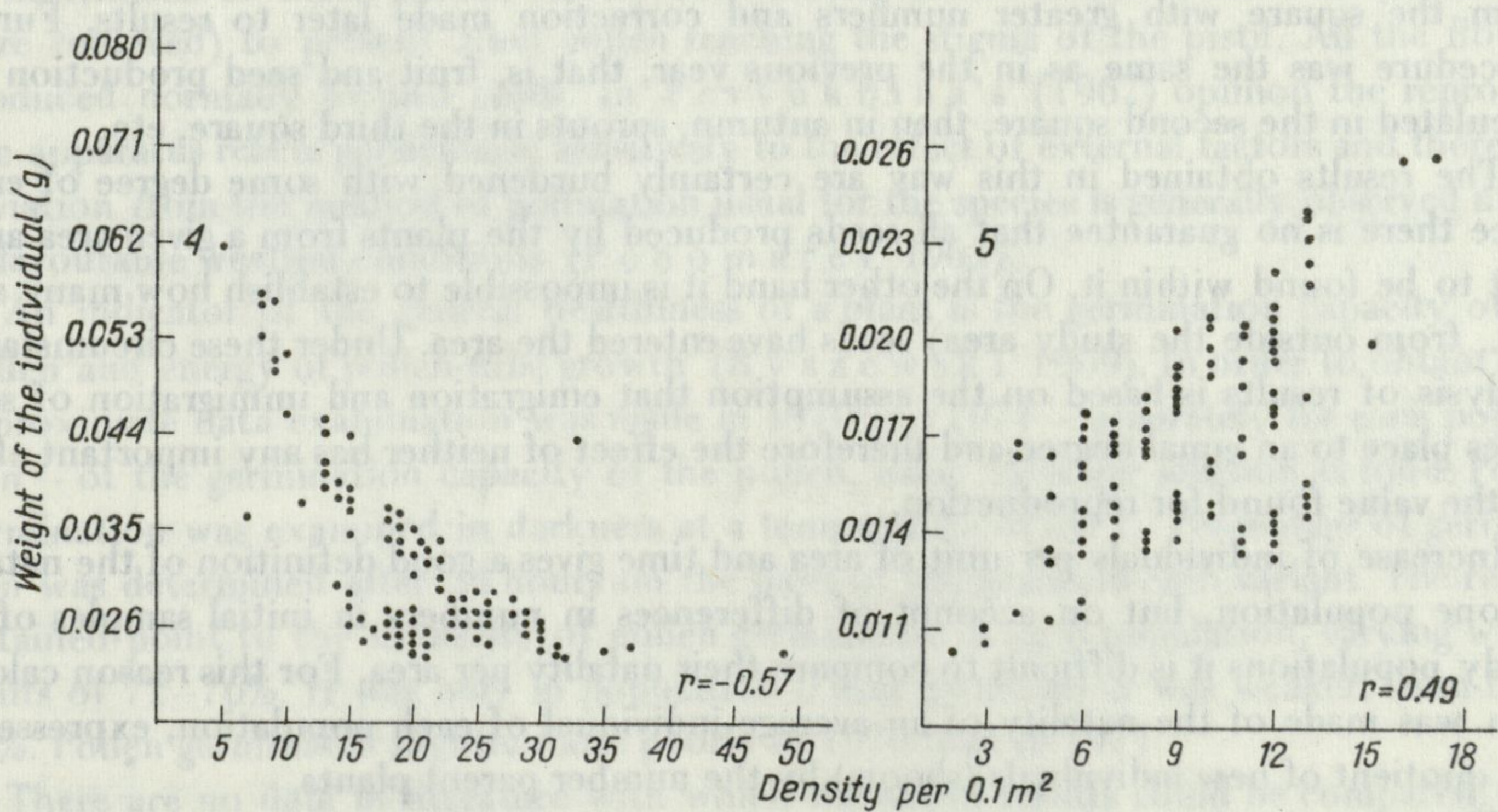


Fig. 12. Diagram of relation between weight of an individual and density (populations 4 and 5)

3.3. Natality

3.3.1. Premises and methods

The second unusually important attribute of a population, in addition to density, is its capacity for reproduction. In a wider sense it includes the production by any given organism of new individuals, irrespective of the way in which they arise. In population terminology distinction is made between the concept of "maximal" natality (= "absolute") and "ecological" natality (= real or, quite simply, natality). The first term defines the maximum number of individuals produced under ideal conditions, without the unfavourable effect of habitat pressure; maximal natality is a constant value for the given population describing the biotic potential of the individuals forming it. In practice this value is attained with a considerable degree of approximation and the highest reproduction amongst those found over the whole study period is considered as such (O d u m 1963). Ecological natality applies to real population growth taking place under definite conditions and thus with the participation of limiting habitat factors. It is usually expressed as increase in new individuals per unit of area and time, or else as the number of new individuals produced by a unit of population (one individual in a defined time).

Measurements of natality of five populations of *Spergula vernalis* were made from 1969 to 1971. In May 1969 four identical squares, with a known identical number of individuals, were set up on each stand: the area of each square was 4 m². Each square was divided into four smaller squares, equal units which were analyzed separately. During the fruiting period examination was made within each population of fruit and seed production in the first square: in the autumn of the same year sprouts were counted in the neighbouring second square. The maximum number of sprouts formed the measure of natality. In May 1970 adult individuals were counted in the second and third squares. If density differed in the two squares, an appropriate number of individuals was removed from the square with greater numbers and correction made later to results. Further procedure was the same as in the previous year, that is, fruit and seed production was calculated in the second square, then in autumn, sprouts in the third square, etc.

The results obtained in this way are certainly burdened with some degree of error, since there is no guarantee that all seeds produced by the plants from a given area are in fact to be found within it. On the other hand it is impossible to establish how many alien (i.e., from outside the study area) seeds have entered the area. Under these circumstances analysis of results is based on the assumption that emigration and immigration of seeds takes place to an equal degree and therefore the effect of neither has any important effect on the value found for reproduction.

Increase of individuals per unit of area and time gives a good definition of the natality of one population, but on account of differences in numbers in initial samples of the study populations it is difficult to compare their natality per area. For this reason calculation was made of the natality of an average individual of each population, expressed as the quotient of new individuals (shoots) by the number parent plants.

The measure of reproduction is the resultant of a whole group of factors forming the property either of the plant itself or habitat conditions. Among the more important

questions taken into consideration in this study and arising from the effect of natality we may include: flowering biology, production of fruits and seeds, weight and caloric value of seeds and their capacity for and energy of germination.

3.3.2. Flowering biology

The development of flowers of *Spergula vernalis* takes place gradually from bottom to top of the inflorescence; flowers are usually smaller in the upper parts and often very weakly developed. The flowering time of one flower is short, usually from 4 to 5 days in the lower parts of the inflorescence and 2–3 days in the upper. The unusual regularity in daily rhythm of opening of the flowers is interesting; they open abruptly about 12.30 and equally abruptly close about 15.30.

The observations made point to the frequently encountered variability of means of pollination in angiosperms (S z a f e r 1956, M o w s z o w i c z 1970). Small, unimpressive, scentless flowers gathered into inflorescences, light, loose and abundantly produced pollen, the smooth surface of the pollen and relatively long filaments are evidence of an anemophilous way of pollination (D y a k o w s k a 1959, F a e g r i and I v e r s e n 1964), but the possibility of entomophily cannot be ruled out. During the flowering period of *Spergula vernalis* thrips (*Thysanoptera*), adapted to living in a dune biotope and feeding on its pollen, visit its flowers particularly frequently (G r o m a d s k a 1954). The following species of this group were found on the flowers of the study species: *Chirothrips manicatus* Hal., *Halothrips acanthoscalis* Karny and *Frankliniella intonsa* Tryb. *Philanthus vanans* Payk. also often appeared there, and from time to time hymenopterans.

Entomophily often takes place parallel to anemophily in many species (P o r s h 1956).

In addition to cross-pollination, experiments showed that *Spergula vernalis* is capable of autogamy. During the phase preceding flowering cellophane hoods were placed on 25 individuals of these plants, closely surrounding the ultimate of one bud (the others were removed) to prevent alien pollen reaching the stigma of the pistil. All the flowers produced normally formed seeds. In P e r v u k h i n a's (1967) opinion the reproductive apparatus reacts particularly sensitively to the effect of external factors and therefore deviation from the method of pollination usual for the species is generally observed under unfavourable weather conditions (P o n o m a r e v 1961).

An indicator of the general healthiness of a plant is the germination capacity of the pollen and energy of pollen-tube growth (B y s z e w s k i 1969). In order to obtain even approximate data examination was made in 1970 and 1971 – separately for each population – of the germination capacity of the pollen, using 5% sugar solution as food. Pollen germination was examined in darkness at a temperature of 20°C. Percentage of germination was determined after 24 hours on the basis of 100 grains in each variant. The results obtained point to the similarity of pollen germination in each population, varying within limits of 71–76%. It was only in population 5 that germination was weaker, from 60 to 65%. Pollen germinated slightly more poorly in 1970 than in 1971.

There are no data in literature with which the above results could be compared. It is, however, possible to risk the statement that they form evidence of a high degree of vitality of the pollen of *Spergula vernalis*.

3.3.3. Weight and caloric value of seeds

3.3.3.1. Methods

The weight of seeds defines their good form and thus describes the quality of the material for sowing. Salisbury (1942) draws attention to the particular importance of the weight of seeds in the case of pioneer dune vegetation. The heavy weight of seeds ensures that the plant is not only able to expand, but provides chances of transfer to more highly organized communities (Salisbury 1942, Zarzycki 1964).

Although the weight of seeds gives some indications as to the contents of store material, nevertheless these two parameters are not always characterized by positive correlation (Falińska 1969a). On this account it is better to estimate seeds on the basis of their caloric value for purposes of comparison (Phillipson 1969).

The weight of 1000 seeds of five populations was defined in accordance with generally accepted international regulations (Dorywalski, Wojciechowski and Bartz 1964), bearing in mind that the difference between the maximum and minimum weight of each hundred seeds did not exceed 10% of the mean value.

Seeds from about 200 plants on each stand were taken for determining caloric value. After preparing the material by means of the method given by Górecki (1965), the samples were burnt in a Phillipson (1964) miniature bomb calorimeter; measurement of the heat of burning was read by means of a Kipp Zonen BD 5 micrograph. In addition homogenized material was burnt in a muffle furnace at a temperature of 800°C to a constant weight in order to determine the percentage of ash content.

3.3.3.2. Discussion of results

The weight of 1000 seeds and caloric value of seeds from the study populations are set out in Table IV. Heat of burning is given in relation to 1 g of dry mass and — after allowing correction for ash — converted to 1 g of organic material.

Tab. IV. Comparison of weight and caloric value in five populations

Popula- tion	Weight of 1000 seeds (mg)	Ash content (%)	Caloric value of seeds	
			cal/g of dry mass	cal/g of organic substance
1	180.5 ± 0.002	4.9	3925.0 ± 40.0	4127.2
2	126.6 ± 0.001	5.1	4193.0 ± 18.5	4422.9
3	144.6 ± 0.002	5.2	4165.0 ± 18.2	4388.8
4	125.0 ± 0.002	5.2	4329.0 ± 68.0	4566.4
5	130.1 ± 0.003	5.0	4263.1 ± 18.0	4487.5

It can be seen from Table IV that while the weight of seeds from one population is a character which varies very little, there are statistically significant differences between the populations compared. The largest seeds were found in population 1

Tab. V. Production of fruits and seeds in five populations in 1969–1971

Popu- lation	Year	Production of fruits (number)				Production of seeds (number)				
		per 1 m ²		per individual		per 1 m ²			per individual	
		non- -branching individuals	branching indi- viduals	non- -branching	branching	non- -branching individuals	branching indi- viduals	jointly	non- -branching	branching
1	1969	226.4	482.9	5.0 ± 0.10	19.4 ± 3.8	5887.7	12312.8	18200.6	130.3	496.5
	1970	217.8	367.5	4.4 ± 0.18	15.0 ± 3.8	5445.0	8731.8	14176.8	110.0	356.4
	1971	256.7	596.5	5.6 ± 0.16	20.2 ± 4.3	6673.7	16141.0	22814.7	145.1	547.1
2	1969	1107.7	1835.4	6.0 ± 0.05	19.3 ± 3.7	43199.5	62109.9	105309.5	234.8	653.8
	1970	1196.4	1701.4	6.4 ± 0.19	16.7 ± 3.6	45478.4	52878.3	98356.7	243.2	518.4
	1971	1340.8	2038.4	7.0 ± 0.20	19.1 ± 3.9	52291.1	70427.1	122719.1	273.8	653.6
3	1969	572.1	303.3	6.5 ± 0.09	12.5 ± 3.9	20023.8	8042.6	28066.4	225.7	330.9
	1970	495.9	185.4	5.7 ± 0.21	10.0 ± 2.7	16364.7	4626.8	20991.5	188.1	250.1
	1971	461.4	316.3	6.3 ± 0.17	15.1 ± 3.9	15686.2	8482.1	24168.3	214.9	403.9
4	1969	1437.3	715.1	7.9 ± 0.07	15.2 ± 5.0	53175.6	20450.7	73626.3	290.4	436.2
	1970	1365.0	493.9	7.5 ± 0.27	11.8 ± 4.7	50505.0	13582.3	64087.2	277.5	323.2
	1971	1769.0	789.6	9.7 ± 0.22	16.8 ± 4.5	67225.8	24493.4	91719.2	369.4	521.2
5	1969	330.6	107.7	3.9 ± 0.06	8.8 ± 2.9	7934.8	2575.2	10509.9	91.8	209.2
	1970	316.0	68.0	4.0 ± 0.13	6.5 ± 2.8	7584.0	1355.3	8939.4	96.0	129.1
	1971	331.6	96.7	4.6 ± 0.16	8.7 ± 2.6	7959.1	2277.7	10236.8	110.1	207.2

and the lightest in populations 2 and 4. These results lead to two basic conclusions: (1) tall individuals growing in a dense community produce relatively light seeds and (2) the weight of seeds does not exhibit a positive correlation with growth and general formation of the vegetative parts of a plant. The results thus provide confirmation of the opinion held by Salisbury (1942) and Zarzycki (1964), according to which the weight of seeds exhibits a negative correlation with the density of the individuals producing them. The properties of the biotope are of secondary importance in this respect (Salisbury 1942).

In general, it can be said that as in the case of the majority of annual plants growing in open communities, the seeds of *Spergula vernalis* are very light, and differ greatly from the similarly sized seeds of annual species of meadows or forests (cf. Salisbury 1942, Zarzycki 1964).

The results also point to the absence of a direct connection between caloric value of seeds and their weight. The small, light seeds of population 4 have a higher energetic value than the far heavier seeds of population 1. There are statistically significant differences between the heat of burning seeds from population 4 and 1, and 5 and 1; the remainder are similar in this respect.

Comparison of the results obtained with data in literature (Golley 1961, Ken-deigh and West 1965, Falińska 1969a) leads to the conclusion that the caloric value of the seeds of *Spergula vernalis* is relatively low which may be due to the effect of the poor biotope in which it grows. It is difficult to give a more exact interpretation of results as the whole group of factors affecting the caloric value of seeds is not as yet fully known.

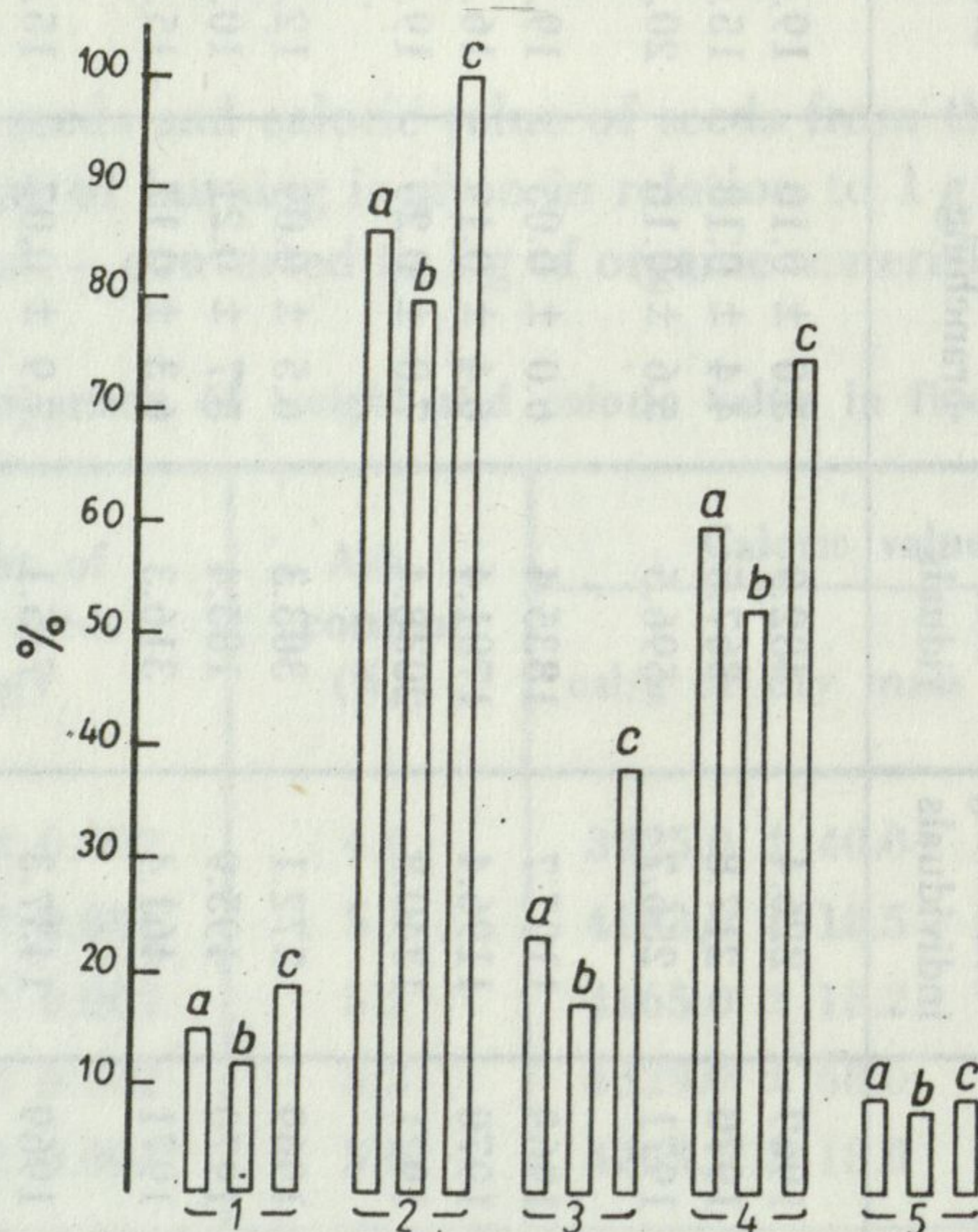


Fig. 13. Seed production per 1 m² in five populations

a — in 1969, b — in 1970, c — in 1971.

100% — productivity of population 2 in 1971

3.3.4. Fruit and seed production

3.3.4.1. Methods

Production of fruits and seeds was measured in five populations during the period 1969–1971, taking into consideration two aspects of the question: average production of one individual in the population and total production of fruits and seeds per unit of area.

The first value was obtained by analysing 100 branching and 100 non-branching individuals, selected at random from the areas marked out for examination of natality. Calculations of individual production per total number of individuals from an area of 1 m² gave the production of fruits and seeds per unit of area. The results are set out in Table V and Figure 13.

3.3.4.2. Discussion of results

Even a superficial analysis of the results obtained shows that production of fruits and seeds is high both in relation to one individual and to unit of area. The enormous production of small seeds is characteristic of the majority of plants growing in open communities (Salisbury 1942, Sen 1968). Its abundance is particularly strikingly apparent in comparison with the low seed production of forest species (Zarzycki 1964, Falińska 1969b).

Taking into consideration the total number of seeds per 1 m² very great differences can be seen in the populations compared, due primarily to the uneven character of population density and percentage of branching individuals. For purposes of comparison, if the maximum production of seeds found on stand 2 in 1971 is taken as 100% (122,719.1 per 1 m²) in the same year population 1 produces 18.6% of this figure, population 3 – 38.3%, population 4 – 74.7%, population 5 – 8.3% (Fig. 13).

Individual production is interesting as its results point to two relations: (1) higher, more luxuriant plants produce more seeds and (2) seed production – within the limits of the densities observed – is positively correlated with population numbers which forms a deviation from the general rule of inverse proportions (Salisbury 1942, Knapp 1954, Zarzycki 1965) of the two values.

Differences in seed production in the years compared are due chiefly to the varying number of fruits, the number of seeds in one sac is a fairly stable character within one population, and is not subject to the effect of climatic conditions. Apart from a few exceptions fruit and seed production was highest in 1971, and lowest in 1969.

It must be added that the fraction of fruiting individuals is generally equal to the number of individuals, and it was only in population 5 that the percentage of fruiting was slightly lower, being 95–97% for the total number of individuals.

3.3.5. Seed germination capacity and energy under laboratory conditions

3.3.5.1. Methods

Examination of germination capacity and energy of seeds from five populations was made in 1969 and 1970, placing them on highly hygroscopic filter paper in a Petrie dish. The duration of the resting period was established by means of the germination results of

“trial series” set up every two weeks from the time the seeds were collected. Mature seeds, either not cooled or cooled at a temperature of 5°C for 7 days, germinated in three variants: under constant lighting conditions, alternate light and darkness and complete darkness at a temperature of 18–22°C. Three repeats were made of each variant. Results are given in Table VI.

Tab. VI. Germination capacity and energy of seeds under laboratory conditions

Popu- la- tion	Germination capacity (%)						Germination energy (after Pieper)
	uncooled seeds			cooled seeds			
	alternate light conditions	total darkness	contin- uous light	alternate light conditions	total darkness	contin- uous light.	
1	41.3 ± 2.6	5.3 ± 0.5	1	10.0 ± 1.5	1	0	15.7 ± 1.6
2	44.3 ± 3.8	8.0 ± 0.6	0	14.0 ± 1.1	2	0	15.6 ± 1.1
3	36.7 ± 1.8	4.5 ± 0.7	0	9.0 ± 1.5	0	0	18.3 ± 1.9
4	54.6 ± 4.2	9.0 ± 0.8	1	18.0 ± 1.0	2	0	15.5 ± 1.7
5	24.9 ± 0.7	3.0 ± 0.5	0	6.0 ± 1.0	0	0	18.4 ± 2.0

3.3.5.2. Discussion of results

The period of absolute rest of the seeds of *Spergula vernalis*, measured from the time of their production to the appearance of the first sprouts, was about 85–90 days under both field and laboratory conditions. Maximum germination capacity was reached by seeds kept under room conditions after about 120 days, thus full “after-ripening” (F o r m a n o w i c z o w a and K o z ł o w s k i 1967) was observed later than under natural conditions.

The results of the experiments point to the relatively low germination capacity of the seeds of *Spergula vernalis* and – in extreme cases – to considerable differences between the populations compared. The highest percentage of live seeds was found in population 4, almost three times less in population 5. In comparison with population 4 only the seeds of population 2 fail to differ to a statistically significant degree in respect of vitality.

The results presented above relate to germination of seeds which were not subjected to cooling and kept under varying light conditions. In darkness minimal germination takes place, and under constant light conditions almost completely fails to take place at all.

Cooling of seeds was found to reduce germination capacity by 3–4 times.

Germination energy, calculated according to Pieper’s equation (D o r y w a l s k i, W o j c i e h o w s k i and B a r t z 1964), is similar in the populations compared – none of the differences are statistically significant. The shortest time required for germination of 1 seed was found for population 4, then 2 and 1, and is therefore positively correlated with the vitality of seeds.

Tab. VII. Comparison of natality in five populations in 1969–1971

Population	Year	Number of parent individuals per 1 m ²	Number of new individuals per 1 m ²	Germination of seeds (%)	Number of new individuals per 1 parent individual	Percentage of maximal natality
1	1969	70.0 ± 7.5	257 ± 20.5	1.42	3.67	77.2
	1970	74.0 ± 6.6	228 ± 27.1	1.61	3.08	64.8
	1971	75.5 ± 6.7	359 ± 27.9	1.57	4.75	100.0
2	1969	279.0 ± 20.4	896 ± 33.9	0.85	3.21	67.5
	1970	289.0 ± 21.8	910 ± 25.0	0.92	3.15	66.3
	1971	297.5 ± 26.0	1292 ± 37.4	1.05	4.33	91.1
3	1969	113.0 ± 14.3	156 ± 19.1	0.56	1.38	29.0
	1970	105.5 ± 10.3	123 ± 16.2	0.58	1.16	24.4
	1971	94.0 ± 9.1	146 ± 10.6	0.60	1.55	32.6
4	1969	230.0 ± 20.4	312 ± 25.8	0.42	1.30	27.4
	1970	224.0 ± 18.0	308 ± 32.3	0.48	1.37	28.8
	1971	229.0 ± 22.6	489 ± 33.0	0.53	2.13	44.8
5	1969	96.0 ± 9.2	137 ± 14.5	1.30	1.42	29.8
	1970	89.5 ± 7.4	124 ± 15.6	1.39	1.38	29.0
	1971	83.2 ± 8.5	124 ± 14.2	1.21	1.48	31.1

Seeds kept in linen bags at room temperature retain their germinating capacity for a long time, and when sown in Petrie dishes after a lapse of one year their germination was scarcely 20% less than during the period of maximum vitality.

The vitality and requirements of seeds in respect of temperature, moisture of substratum, access to light, etc. are among those species characters which are to a great extent perpetuated. This is shown by the results of Sen's (1968) studies on related species of the family *Asclepiadaceae* originating from a similar desert-like biotope; the author found great differences both in respect of the germination requirements of the seeds and also their vitality and germination energy.

3.3.6. Discussion of results of natality studies

Increase of new individuals per 1 m² of area and the natality of an average individual in a population are illustrated by Table VII. In order to facilitate comparison of populations the number of parent individuals is also given in Table VII, the percentage of germination of seeds and — expressed in percentages — the ratio of real natality of an individual of each population to the approximate maximal natality, for which it was decided to take the size of population 1 in 1971 as the highest during the study period (Fig. 14).

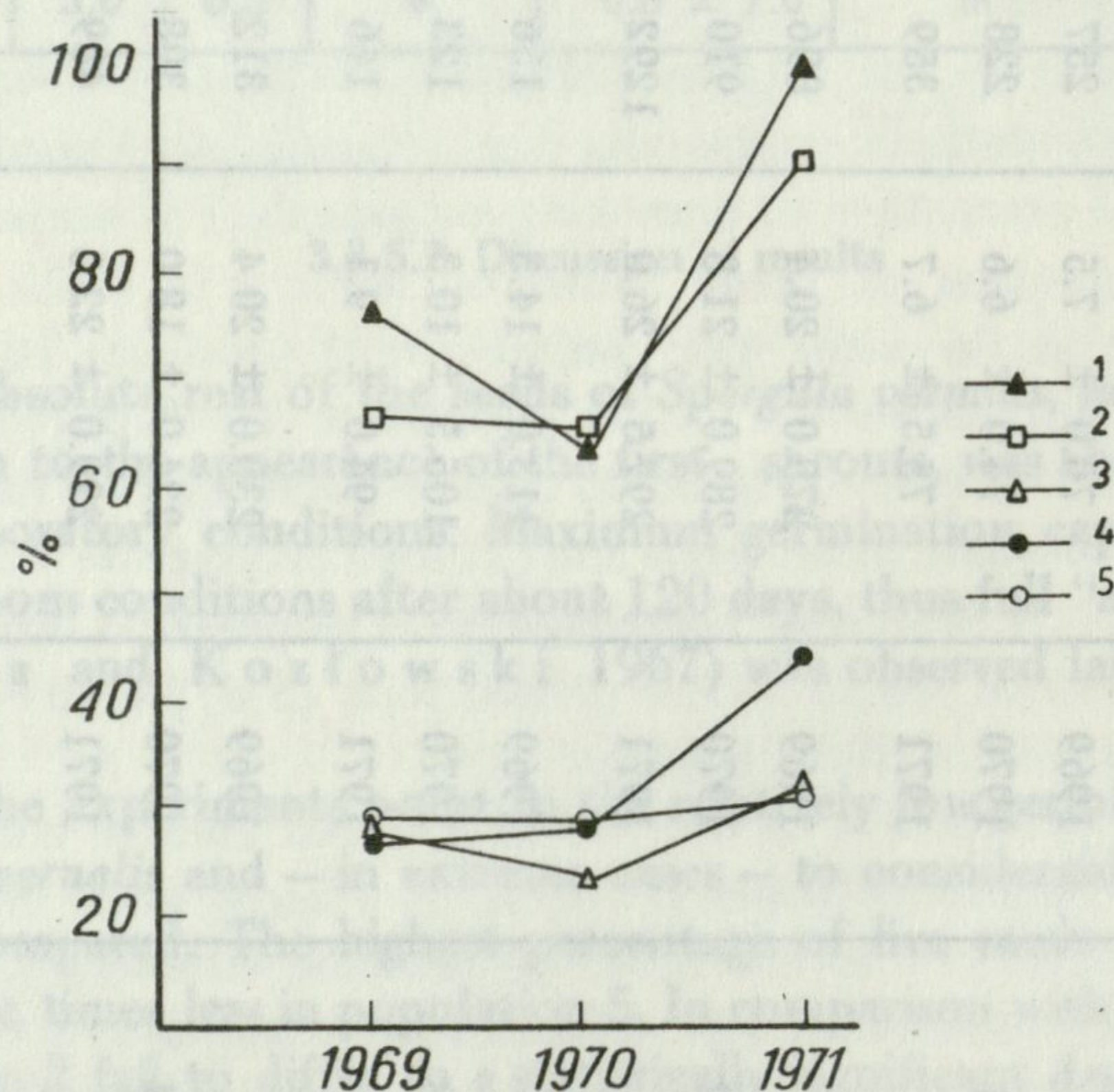


Fig. 14. Ratio of real natality of five populations to maximal natality (100% — maximum natality for study period in population 1 in 1971)

The results point to an unusually low percentage of germinating seeds, particularly in comparison with those observed under laboratory conditions. This phenomenon occurs in the majority of plants and is specially distinct in the case of species producing small seeds (Peplińska 1967); the earlier germination of seeds in their natural habitat than in the laboratory, connected with the physical and mechanical properties of the soil, is also a general rule.

The connection between low percentage of germination and simultaneous enormous production of seeds has also been emphasised by Salisbury (1942), in whose opinion poor germination is primarily due to the high mortality rate among plants in an embryonic state, and depends on habitat conditions to a slight degree only.

The differences between the populations compared in respect of production of new individuals by a unit of population are, in extreme cases, fairly large. The extent of reproduction, as shown by Table VII, is affected both by production of seeds and also their capacity for germination. The factor of density, at least within the range of values observed, is not of importance here, as is shown by the similar, relatively high natality of populations 1 and 2, which differ considerably in respect of density. The natality of the other populations is 2–3 times lower than in the two previous populations.

These results suggest that a factor meriting attention here may be the presence or absence of competitive, alien species. In populations 3 and 4 the low reproduction is most probably also connected with the type of vegetation accompanying *Spergula vernalis*. The compact, dense carpet of mosses and lichens retains a great mass of seeds on their surface, rendering it difficult for them to reach the soil.

When the natality of the populations in the years compared is taken into consideration the higher reproduction in 1971 than in the other years becomes very distinct. The more favourable climatic conditions in 1971 have already been emphasised when discussing fruit and seed production.

3.4. Mortality

3.4.1. Premises and methods

By mortality is meant the rate of disappearance of individuals from a population, that is, the number of individuals dying within a given period. It is usually expressed in percentages of the initial population. As in the case of natality, it is possible to distinguish between the theoretical concept of "minimal mortality" taking place under conditions most favourable to the species, and "ecological mortality" – real mortality defining the disappearance of individuals under definite habitat conditions.

As the physiological age of the plant in question is only 9–10 months, after reaching which it dies as it were a natural death of old age, the disappearance of individuals in various stages of development has been defined in this study: (a) a month after germination – stage of one leaf whorl, (b) after winter rest of one leaf whorl, (c) formation of inflorescence buds, (d) in the full blooming period and (e) in the full fruiting period.

Observations were made from 1969 to 1971 in the squares which had been used for natality studies. The maximum number of germinated seeds per 1 m^2 was taken as the initial unit.

3.4.2. Discussion of results

Survivorship curves expressed in percentages of the initial numbers of each population are illustrated in Figure 15.

The results point to fairly considerable differences between the populations compared, both in respect of the percentage of surviving individuals and the period of particularly

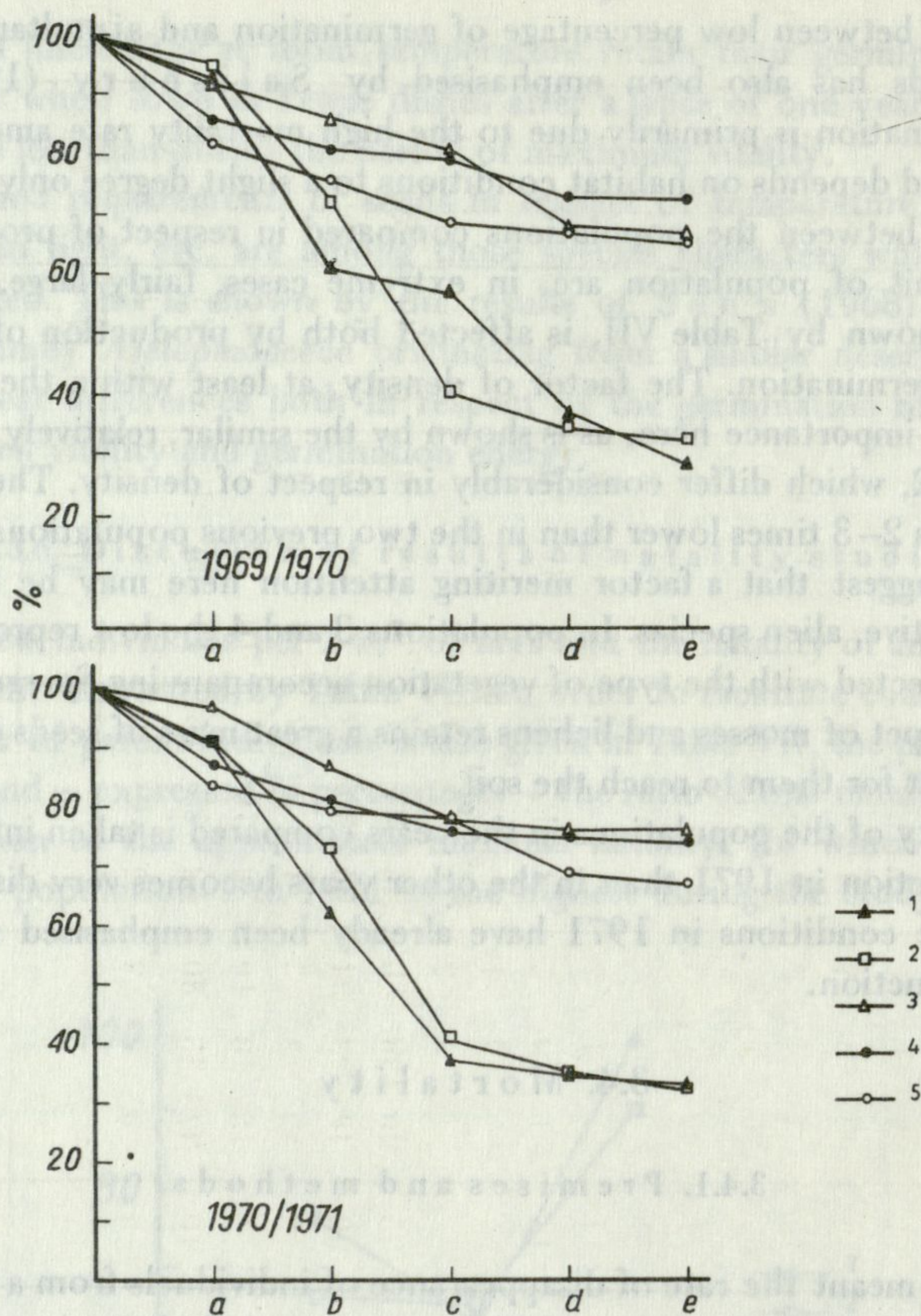


Fig. 15. Survivorship curves for five populations

100% — number of germinated seeds per 1 m². a—e — development stages: a — month after germinating — stage of 1 leaf whorl, b — after winter rest — stage of 1 leaf whorl, c — before buds of inflorescence form, d — during mass flowering period, e — during mass fructification period

intensive mortality. A character which all populations had in common was the high mortality rate in winter. This phenomenon is connected on the one hand with the juvenile age of the plant, usually characterized by increased mortality, and on the other by unfavourable climatic conditions. The harmful effect of frost is very distinct, particularly in relation to the scantily covered stands of populations 1 and 2, where the numbers of individuals disappearing in winter are especially great. After forming the III leaf whorl mortality is minimum among individuals in populations 3 and 4, and further a fairly large number of dying individuals is observed in the other populations generally characterized by the smallest percentage of survival.

The high mortality rate among plants in populations is a frequently observed phenomenon in nature (Zarzycki 1965). The survival of certain individuals and death of others is usually attributed to individual differentiation of the population into weaker and stronger individuals from the beginning of their lives (Morozow 1953, Sukachev 1953). In the given case the effect of the microbiotope is also distinct, and it

is to them, as shown by observations, that the high mortality rate among individuals in populations 1 and 2, during a period when the other populations had already maintained more or less constant numbers, that the high mortality rate should primarily be attributed. The scanty cover of vegetation adapted to stabilizing windborne sands, of stands 1 and 2, favours the deflation processes and accumulation of sand during the period of a windy and dry late spring. The correctness of this view is supported by the fact that individuals in the closest vicinity to clumps of *Corynephorus canescens* (L.) P. B., or else forming large clumpings better adapted to struggle with sand, were the ones to survive. The remainder were either buried under sand or died as the result of exposure of their root system.

In the case of population 5 the disappearance of individuals was to a certain extent due to a plant disease caused by the fungus *Peronospora vernalis* Gäum. Towards the end of April and in May the mass appearance of coniciophores and conidia was observed on the leaves of the study plant. *Peronospora vernalis* has so far been given for only a few stations, from Silesia, from the western part of the Wielkopolska district and the Masovian region (Kochman and Majewski 1970). Not a single case of plants being invaded by fungus was found on the remaining stands.

Mortality among populations in the years compared was in general similar, being slightly lower only during the growing season of 1970/1971.

3.5. Net growth index of the populations

3.5.1. Premises

By comparing natality and mortality of a population we obtain the final result (net) of its growth describing the absolute increase or decrease of a population within a unit of time. Definition of the index of growth thus permits of obtaining information as to the tendencies of a population to occupy new areas or to withdraw from those previously occupied.

Calculation has been made in this study of the net natality of each population in 1970 and 1971, the density of individuals per the same unit of area (1 m^2) in 1969 being taken as the initial unit.

3.5.2. Results

Comparison of growth indexes for the study populations is illustrated in Figure 16, but as they refer to three years only they most certainly do not permit of drawing detailed and exact conclusions. It is only possible with a considerable degree of caution, to indicate the tendencies manifested by the different populations. Density varies to the least degree in population 4: the index of growth describing net natality in this population is close to one. A systematic decrease in number of individuals is evident in populations 5 and 3, and growth in populations 1 and 2. In general, however, the results point to fairly intensive autoregulation of each population. The high mortality rate is, as it were compensated for by increased natality (populations 1 and 2) and the low percentage of germination by large production of seeds (populations 3 and 4), etc.

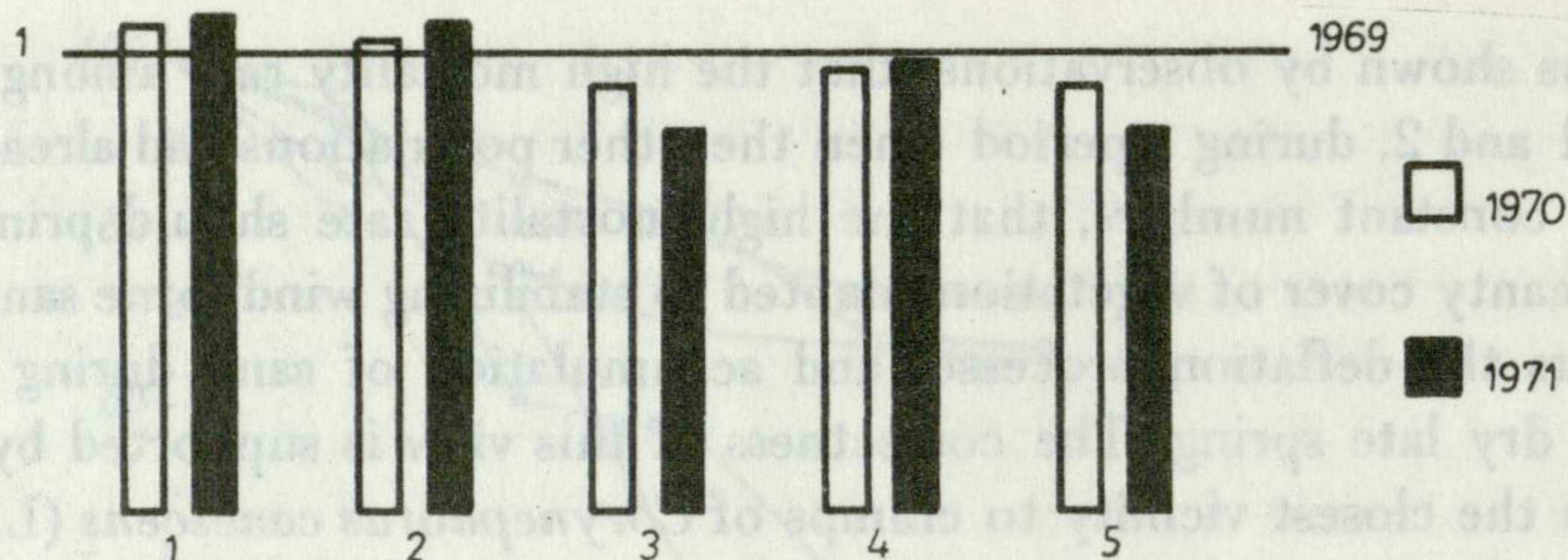


Fig. 16. Index of growth in five study populations in 1970 and 1971 (comparative unit is population numbers in 1969)

Using the terminology proposed by V a s i l e v i c h (1970) we can allocate changes in density in population 4 to the oscillation type with the slight fluctuations in the region of the mean characteristic of it; the remaining populations represent the successive type, that is, the type exhibiting a tendency in a given direction in respect of changes in numbers, and in consequence leading either to complete disappearance of a species, or to constant (up to a certain limit) increase in density.

4. CONCLUSIONS

Limitation of the studies to a relatively small area does not justify generalizing on the basis of all the results obtained, nevertheless a similar biotope to that with which the plant is connected over the whole of its range gives grounds for considering that many of the properties observed of the *Spergula vernalis* populations belong to characteristic features of the species.

Detailed discussion of results has been given in successive sections of this paper. It is, however, worth while emphasising those moments which relate to interrelations between the plant and the biotope and provide information on the relations occurring between organisms within a population.

The results of these studies suggest the following conclusions:

1. The occurrence of *Spergula vernalis* solely on dry, poor, biotopes would appear to be due not only to the modest food requirements of this species but primarily to its low competitive capacity. This assumption is confirmed by studies of population numbers and biomass. The favourable effect of the richer biotopes continues to be evident for as long as the interspecies competition factor fails to occur.

2. Studies of the spatial structure of five populations of *Spergula vernalis* show that: (a) a clumped type of distribution of individuals in space occurs in each population and (b) the lesser the degree to which the dunes are stabilized, the greater the degree of crowding. Clumping of individuals is due not only to the way in which the seeds are scattered, but is also evidence of the reaction of a population to the destructive effect of windblown sand. The percentage of branched individuals is greater on rewinnowed biotopes than in populations on the stabilized parts of the dune.

3. Population density does not affect the extent of reproduction, but distinctly influences the weight of an individual. Up to a certain limit of densities the two parameters rise together, and it is not until a considerable number of individuals per unit of area are reached that a negative correlation is evident.

4. Slight changes in density within one population, found in successive years, are evidence of fairly intensive autoregulation; the role of leading factor in regulating population numbers is played by mortality.

5. Production of seeds, their size, caloric value and germination capacity come within the limits characteristic of the majority of annual plants in open communities.

6. The natality of a population is primarily dependent on extent of seed production and seed germination capacity. The effect of habitat conditions on the reproduction of a population is indirect and of secondary importance.

7. Comparison of survival curves for the five populations shows that the biotope exercises a decisive influence in this respect. In principle two facts contribute to the high mortality rate of a population on weakly stabilized sands: (a) the ease with which scantily covered soils dry up and (b) the destructive effect of windborne sand. Our observations have shown that it is mainly individuals in the immediate vicinity of clumps of *Corynephorus canescens* which survive, form large clumps and are strongly branched. The harmful effects of food competition are in this case more than compensated for by the benefits gained from individuals occurring in a group.

8. The value of the population increase index is dependent on the course taken by the process of the spread of vegetation over the dunes. *Spergula vernalis*, as a pioneer species, rapidly occupies bare sands. As the latter become stabilized and the soil is enriched by humus *Spergula vernalis* retreats from areas it previously occupied, giving way to other species of greater competitive strength. The study period was, however, too short to permit of drawing completely unequivocal conclusions.

I am greatly indebted to Professor Dr. K. Zarzycki for his help and guidance during the preparation of this study. I must also express my thanks for consultations and guidance to Professor Dr. J. Szwejkowski, Doc. Dr. J. Staszkievicz, Doc. Dr. R. Bohr and Dr. J. Wilkoń-Michalska, and I am also extremely grateful to Professor Dr. Z. Prusinkiewicz and Dr. W. Plichta for their assistance in interpreting the results of soil analyses.

5. SUMMARY

The paper presented here is the first in a cycle of studies on the ecology and morphological variations in *Spergula vernalis*. It contains the results of analysis of group properties in five populations of *Spergula vernalis* in relation to abiotic and biotic habitat conditions. The studies were made from 1969 to 1971 in a successive sequence of dune stands in the Toruń Basin. The chosen areas differed from each other both in respect of the degree of plant cover and composition of their flora (Fig. 3, 7), and also the different physical (Fig. 5, 8) and chemical (Tab. I) properties of the soils. They were also distinguished – in extreme cases – by a slightly different microclimate (Fig. 6).

The scope of the studies included the density, spatial structure, natality, mortality and net growth index of the populations.

Analysis of density took into consideration frequency, numbers of individuals per unit of area and biomass – determining the participation of the various organs of the plant. Coefficients of correlation for the average weight of an individual and population density were calculated. Evaluation of the horizontal structure of the populations was supplemented by examination of the degree of crowding of individuals.

Natality of the populations was examined in detail on the basis of the following: flowering and fruiting biology, germination capacity of pollen, seed production, weight and caloric value of seeds, germination capacity and energy of seeds.

Mortality in the populations was examined in several stages of the ontogenesis of *Spergula vernalis*. The index of net growth of each population was calculated on the basis of results of natality and mortality.

The studies made showed that:

1. Abundance and biomass of the study populations depend not only on the degree to which the biotope is rich in nutrient components, but primarily on the presence or absence of other species competing with *Spergula vernalis* for space and food. The favourable effect of richer biotopes continues to be evident until the interspecies competition factor appears (Tab. II, III, Fig. 9).

2. The weight of an individual exhibits a distinct connection with population density. In very dense populations a statistically significant negative relation was found between the two parameters; with low densities the coefficients of correlation are positive (Fig. 10, 11, 12).

3. The mass of fruits forms about 50% of total biomass, while root mass does not usually exceed 10% (Tab. II). In Salisbury's (1952) opinion such proportions are characteristic of the majority of annual plants in open communities.

4. Studies of the spatial structure of five populations showed that a clumped type of distribution of individuals in space occurs in each population (Tab. III). The degree of crowding is greater where the sands of the dunes are less firmly stabilized. The clumping of individuals is evidence of their reaction to the destructive effect of windborne sand; it is due to a lesser extent to the way seeds are disseminated.

5. The flowers of *Spergula vernalis* are both anemophilous and entomophilous; in addition autogamy was found as well as cross-pollination. The percentage of pollen germination is fairly high, coming within limits of 60–76%.

6. The weight of seeds exhibits a negative correlation with the density of the individuals producing them; it depends on the properties of the biotope to a slight degree only. Like the majority of annual plants of open communities, the seeds of *Spergula vernalis* are very light in weight (Tab. IV).

7. The caloric value of seeds is relatively low (Tab. IV), not exhibiting any direct connection with the weight of seeds.

8. Seed production – within the scope of the densities observed – is positively correlated with population numbers, which forms a deviation from the general rule of inverse proportions. Climatic conditions affect the production of fruits, but the number of seeds in a capsule is a stable character within one population. Both in relation to one individual and also when converted to a unit of area, production of fruits and seeds by *Spergula vernalis* may be considered as very high (Tab. V, Fig. 13).

9. Population density does not affect the extent of reproduction; the natality of a population depends primarily on the extent of seed production and their germination capacity (Tab. VII) and only indirectly on habitat conditions.

10. The germination capacity of the seeds of *Spergula vernalis* is relatively low, fairly considerable differences being found between the populations compared (Tab. VI). Germination energy is positively correlated with the vitality of seeds.

11. Studies of population mortality showed that the effect of the biotope is decisive in this respect. In principle two factors contribute to the high mortality rate in populations on weakly stabilized sands (Fig. 15): (a) the ease with which scantily covered soils dry up and (b) the destructive effect of windborne sand. It is chiefly individuals forming large clumps, and which are strongly branched, which survive and therefore the harmful results of food competition are in this case amply compensated for by the benefits obtained from individuals occurring in a group.

12. Only slight changes in density were observed within a population in consecutive study years, which is evidence of marked autoregulation: mortality plays the role of leading factor in regulating population numbers.

13. The net value of indexes for the study populations (Fig. 16) become understandable in relation to the process of plants spreading over the dunes. As a pioneer species *Spergula vernalis* rapidly occupies bare sands (populations 1 and 2), but as the latter becomes stabilized and the soil enriched with humus *Spergula vernalis* gives way to species with greater competitive strength (population 5). The study period was, however, too short to make it possible to reach unequivocal conclusions.

6. POLISH SUMMARY (STRESZCZENIE)

Przedstawiona praca jest pierwszą z cyklu prac poświęconych ekologii i zmienności morfologicznej *Spergula vernalis* Willd. Zawiera wyniki analizy grupowych właściwości pięciu populacji *Spergula vernalis* na tle abiotycznych i biotycznych warunków środowiska. Badania wykonano w latach 1969–1971 w sukcesyjnym szeregu stanowisk wydmowych w Kotlinie Toruńskiej. Wybrane powierzchnie różniły się zarówno stopniem pokrycia przez roślinność i składem florystycznym (fig. 3, 7), jak też odmiennym układem fizycznych (fig. 5, 8) i chemicznych (tab. I) właściwości gleb. Cechował je także – w skrajnych przypadkach – nieco odmienny mikroklimat (fig. 6).

Zakres badań obejmował zagęszczenie, strukturę przestrzenną, rozrodczość, śmiertelność oraz wskaźnik wzrostu netto populacji.

Analiza zagęszczenia uwzględniała frekwencję, liczebność osobników na jednostce powierzchni oraz biomasę – z ustaleniem udziału poszczególnych organów rośliny. Obliczono współczynniki korelacji dla ciężaru przeciętnego osobnika i zagęszczenia populacji. Ocenę struktury horyzontalnej populacji uzupełniono zbadaniem stopnia skupiskowości osobników.

Rozrodczość populacji scharakteryzowano w oparciu o szereg zagadnień szczegółowych: biologię kwitnienia i owocowania, zdolność kiełkowania pyłku, produkcję nasion, ciężar i wartość kaloryczną nasion, zdolność i energię kiełkowania nasion.

Zbadano śmiertelność populacji w kilku stadiach ontogenezy *Spergula vernalis*. Na podstawie wyników rozrodczości i śmiertelności obliczono wskaźnik wzrostu netto każdej populacji.

W wyniku badań stwierdzono:

1. Liczebność i biomasa badanych populacji uzależnione są nie tylko od zasobności siedliska w składniki pokarmowe, ale przede wszystkim od obecności lub braku innych gatunków, współkonkurujących ze *Spergula vernalis* o przestrzeń i pokarm. Korzystne oddziaływanie zasobniejszych siedlisk zaznacza się dopóty, dopóki w grę nie wchodzi czynnik konkurencji międzygatunkowej (tab. II, III, fig. 9).

2. Ciężar osobnika wykazuje wyraźny związek z zagęszczeniem populacji. W populacjach o dużym zagęszczeniu stwierdzono istotną statystycznie ujemną zależność obydwu parametrów; przy niskich zagęszczeniach współczynniki korelacji są dodatnie (fig. 10, 11, 12).

3. W ogólnej biomasie około 50% stanowi masa owoców; masa korzeni z reguły nie przekracza 10% (tab. II). Takie proporcje cechuje według Salisbury'ego (1952) większość roślin jednorocznych otwartych zbiorowisk.

4. Badania struktury przestrzennej pięciu populacji wykazały, że w każdej populacji występuje skupiskowy typ rozkładu osobników w przestrzeni (tab. III). Stopień skupiskowości jest tym wyższy, im piaski wydmowe są słabiej utrwalone. Skupianie się osobników świadczy o ich reakcji na niszczące działanie lotnego piasku; w mniejszym stopniu wynika ono ze sposobu rozsiewania się nasion.

5. Kwiaty *Spergula vernalis* zapylane są zarówno anemogamicznie, jak też entomogamicznie; stwierdzono ponadto autogamię obok zapylania krzyżowego. Stopień kiełkowania pyłku jest dość wysoki, waha się w granicach 60–76%.

6. Ciężar nasion wykazuje ujemną korelację z zagęszczeniem produkujących je osobników; w niewielkim stopniu jest on uzależniony od właściwości siedliska. Podobnie jak u większości roślin jednorocznych zbiorowisk otwartych, nasiona *Spergula vernalis* są bardzo lekkie (tab. IV).

7. Wartość kaloryczna nasion jest stosunkowo niska (tab. IV), przy czym nie wykazuje prostego związku z ciężarem nasion.

8. Produkcja nasion – w zakresie obserwowanych zagęszczeń – jest dodatnio skorelowana z liczebnością populacji, co stanowi odstępstwo od generalnej reguły odwrotnych proporcji. Warunki klimatyczne rzutują na produkcję owoców, liczba nasion w torebce jest jednak w obrębie jednej populacji cechą stabilną. Zarówno w stosunku do jednego osobnika, jak też w przeliczeniu na jednostkę powierzchni, produkcję owoców i nasion *Spergula vernalis* uznać można za bardzo wysoką (tab. V, fig. 13).

9. Na wielkość rozrodu nie ma wpływu zagęszczenie populacji. Rozrodczość populacji uzależniona jest przede wszystkim od rozmiaru produkcji nasion i ich zdolności kiełkowania (tab. VII), a pośrednio tylko od warunków środowiskowych.

10. Zdolność kiełkowania nasion *Spergula vernalis* jest stosunkowo niska, przy czym stwierdzono dość wysokie różnice pomiędzy porównywanymi populacjami (tab. VI). Energia kiełkowania jest dodatnio skorelowana z żywotnością nasion.

11. Badania śmiertelności populacji wykazały, że wpływ siedliska w tym względzie jest decydujący. Na wysoką śmiertelność populacji słabo utrwalonych piasków (fig. 15) składają się zasadniczo dwa czynniki: a) łatwość wysychania skąpo porośniętych gleb i b) niszczące działanie lotnego piasku. Przy życiu utrzymują się głównie osobniki tworzące duże skupienia i silnie rozgałęzione, a zatem szkodliwe skutki konkurencji o pokarm są w tym przypadku z nadwyżką kompensowane przez korzyści wynikające z występowania osobników w grupie.

12. W kolejnych latach badań stwierdzono niewielkie zmiany zagęszczenia w obrębie jednej populacji, co świadczy o silnej autoregulacji. Rolę czynnika przewodniego przy regulacji liczebności populacji odgrywa śmiertelność.

13. Wartości wskaźników netto badanych populacji (fig. 16) stają się zrozumiałe w kontekście procesu zarastania wydm. Jako gatunek pionierski *Spergula vernalis* w szybkim tempie opanowuje nagie piaski (populacje 1 i 2). W miarę ich utrwalania i wzbogacania gleby w próchnicę ustępuje miejsca gatunkom o wyższej sile konkurencyjnej (populacja 5). Okres badań był jednak zbyt krótki dla wyciągnięcia jednoznacznych wniosków.

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