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THE PHENOLOGY OF *SPERGULA VERNALIS* WILLD. IN RELATION TO MICROCLIMATIC CONDITIONS

ABSTRACT: This paper contains the results of phenological observations and phenometrical measurements carried out on the ephemeral species *Spergula vernalis* Willd., the studies including both the upper and underground organs of the plant. The results showed which phases are synchronized with climatic conditions and which take place in accordance with the autorhythmicity of the species. Examination was made of the effect of biotope conditions on the start and duration of successive phenophases. The rate of growth of stem and root was traced in relation to the ontogenesis of *Spergula vernalis*.

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1. INTRODUCTION

A detailed analysis of phenophases permits of fairly accurate definition of the ecological requirements of the various species, which result from adaptation of the periods of development to climatic conditions. In addition to climatic factors, the edaphic properties of the biotope also affect the cyclic charakter of plant development (S c h n e l l e 1955), as does also competition between individuals growing on areas covered with dense vegetation (S u k a c h e v 1953). The start and duration of phenophases are to a great degree defined by the autorhythmicity of the species.

The phenological observations and phenometrical measurements made from 1968 to 1971 were aimed at: (a) analysing the periodical development of *Spergula vernalis* Willd., (b) establishing whether the start and duration of successive phenophases of the ephemeral species are synchronized with the climatic seasons of the year, or whether they depend primarily on the autorhythmicity of the plant, (c) showing to what degree and on which phenophases the varying microbiotope conditions of the study stands may exert an either inhibiting or stimulating influence and (d) tracing the rate of growth of stems and roots during the growing season of *Spergula vernalis.*

Studies were made on five dune stands in the Toruń Basin; each of them represented a separate stage in the spread of vegetation over the dune.

2. GENERAL PREMISES AND METHODS

The number of phases to be taken into consideration in detailed studies and the frequency of observations were determined by means of preliminary analysis of the development rhythm of *Spergula vernalis* made during the period 1968/1969 on one stand only (second). A general picture of succession of phenophases was obtained, without taking into consideration the qualitative relation between individuals in different stages of development.

Detailed phenological observations carried out every 3–5 days from 1969 to 1971 included all individuals on an area of 1 m^2 within the five stands chosen for the studies.

The following phenological phases were taken into consideration as best defining the stage of development of *Spergula vernalis:* (1) seedling, (2) one leaf whorl, (3) two leaf whorls, (4) three leaf whorls, (5) buds of inflorescence (they appear simultaneously with the fourth leaf whorl; flower buds are only very faintly distinguishable during this stage), (6) flower buds, (7) early stage of blooming (when the first, i.e. the lowest in the inflorescence, buds open), (8) full blooming (majority of flowers in the inflorescence open), (9) end of blooming (fading of the majority of flowers), (10) last flowers (stage after the majority of the flowers have faded and before the first fruits are formed; usually very short–lived and faintly visible in a single individual), (11) last buds (stage after all flowers have faded and before first fruits form; last buds – situated highest – usually not developing into flowers; short and only faintly visible phase), (12) first unripe fruit, (13) full fructification (metamorphosis of the majority of the flowers in the inflorescence into capsules), (14) ripe fruits and dissemination (from most of the capsules in the fructification), (15) drying up of the plant (individuals at least semi-dry).

While there is no difficulty in determining the vegetative phases, definition of the beginning and end of generative phases can only be made with certain reservations. As is well known, the development of flowers and fruits takes place from the bottom of the inflorescence upwards, the flowers and fruits of one layer developing simultaneously

(B y s z e w s k i 1969). It is therefore possible to observe several parallel phases in one individual, which makes exact definition of its stage of development difficult and in consequence it is necessary to rate certain phenophases as more important and to pay attention to the time at which such a phase dominates in one plant.

Individuals were counted and their phase recorded on each day of the observation period, which permitted of determining the percentage of the units in different phases on the given day.

The results were compared in what is known as phenological spectra, based on the general principles given by B e ï d e m a n (1954), with some of my own modifications. The upper line of the spectrum represents the percentage of appearing and disappearing individuals. The scale is comparable, as the maximum number of individuals given per spectrum in brackets constituted 100% on each stand. The curves obtained in this way permit in the first place of estimating which microbiotope is optimum for the plant and in the second, in which stages of the life of the species it is particularly susceptible to unfavourable conditions.

In order to grasp the participation in percentages of individuals going through the different phenophases on the given day of observation, the current number of individuals was treated each time as 100% and the percentage of individuals in that or another phase was determined in relation to this value. In the vertical direction of the spectrum it is thus possible to read the number of phases recorded on a given day and the percentages of individuals passing through those phases, while the duration of successive phases is recorded in the horizontal direction.

Phenometrical measurements of stem and root length were made as supplementary to phenological observations. During the growing season of 1969/1970 a total of 7 such measurements were made, always taking into account 100 individuals from each stand. The correlation between stem length and root length was also determined. The dispersion of this pair of characters is given in diagram form, the values of correlation coefficients being entered on the diagrams.

As mentioned in the introduction, the studies were made on a successive series of dune stands in the Toruń Basin. A detailed description of the stands is to be found in the study

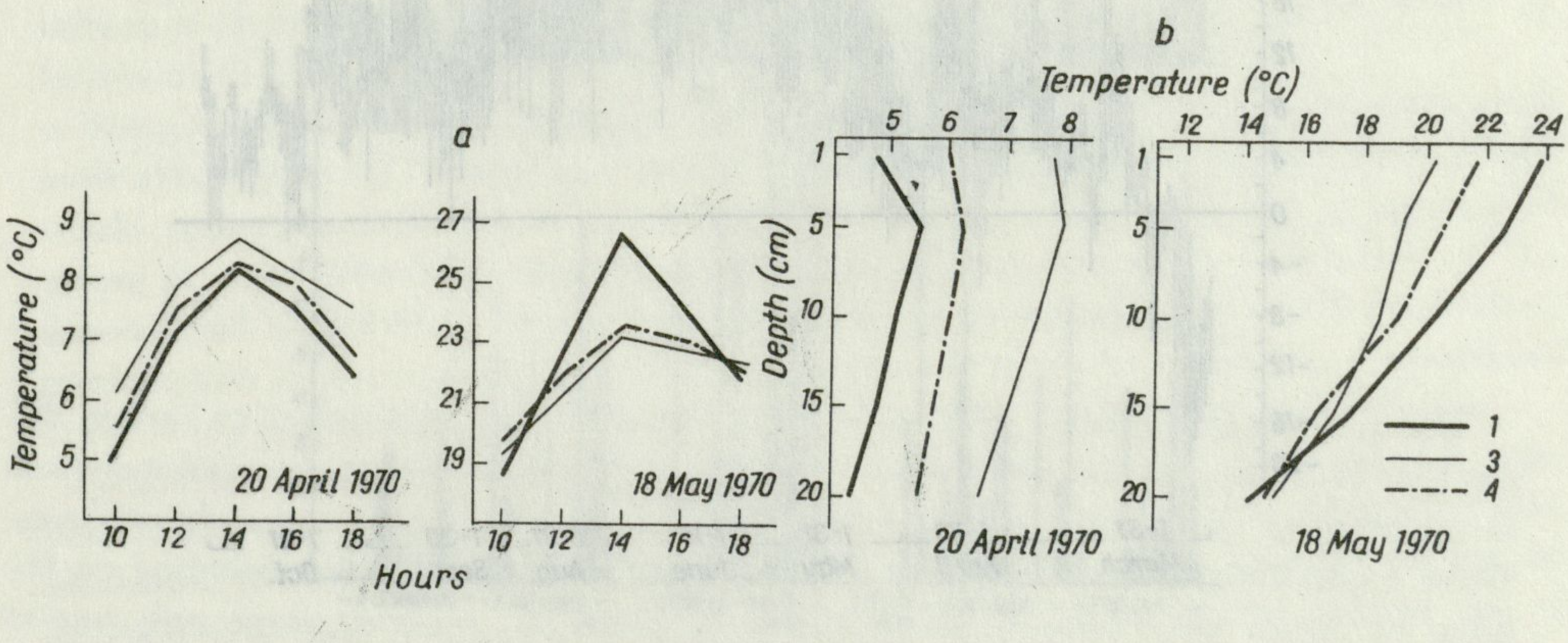

Fig. 1. Comparison of air temperature *(a)* and soil temperature *(b)* on stands 1, 3 and 4

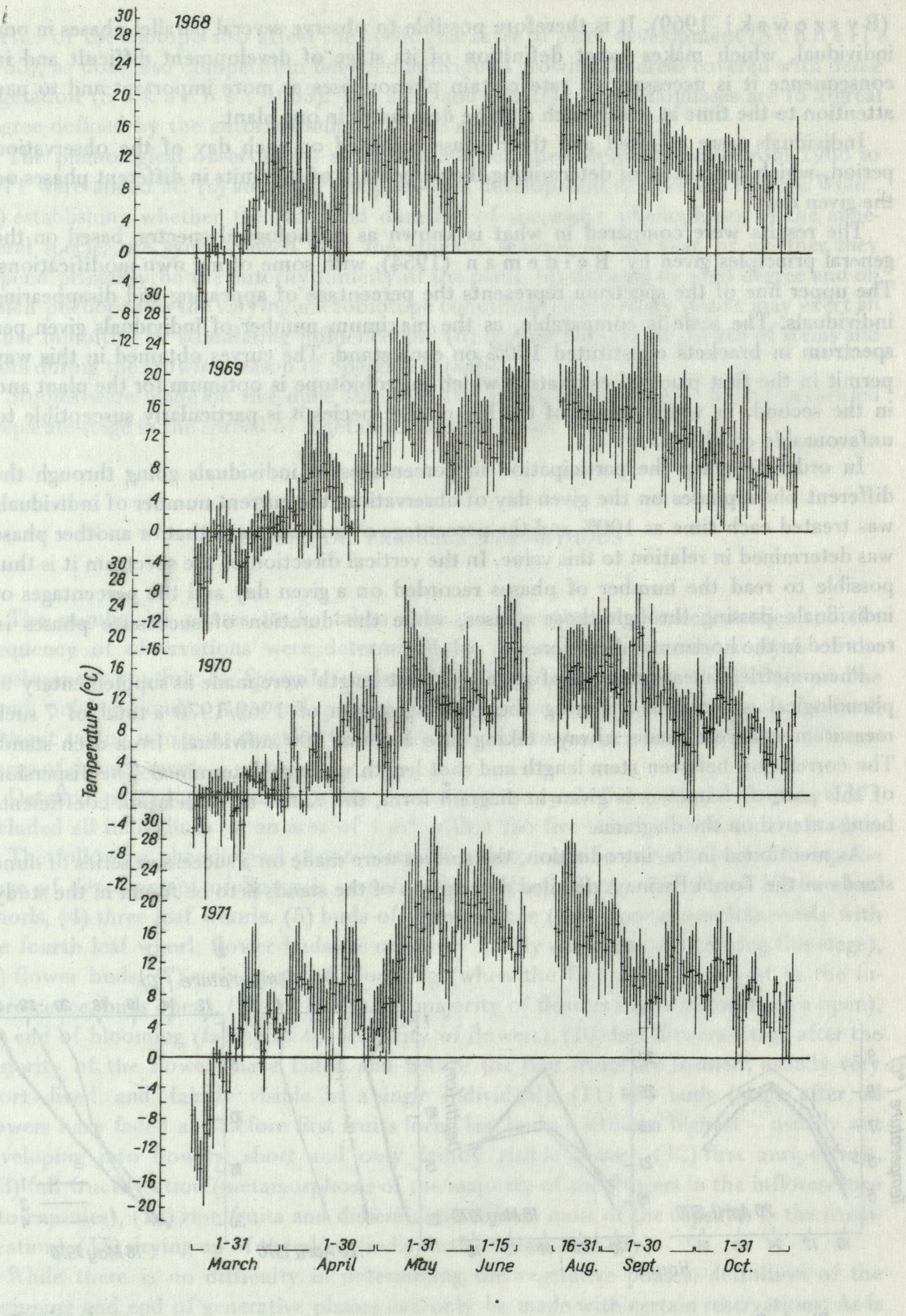

Fig. 2. Minimal, maximal and mean air temperatures from 1968 to 1971 (from 1 March to 15 June and from 16 August to 31 October)

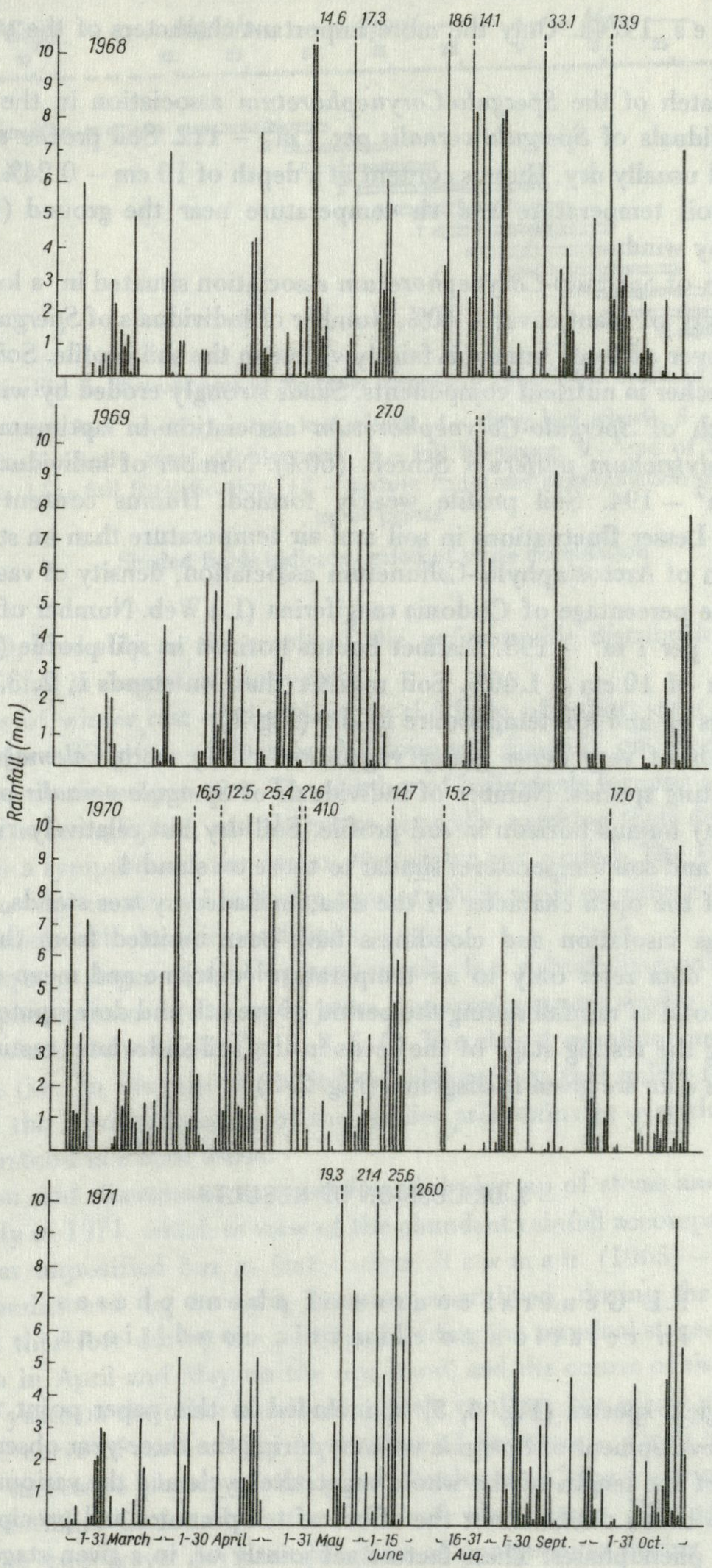

Fig. 3. Total daily precipitation from 1968 to 1971 (from 1 March to 15 June and from 16 August to 31 October)

by S y m o n i d e s 1974a. Only the more important characters of the study areas are given here.

Stand 1. A patch of the *Sperguło-Corynephoretum* association in the initial phase. Number of individuals of *Spergula vernalis* per 1 m^2 – 112. Soil profile unformed; soil very infertile and usually dry. Humus content at a depth of 10 cm – 0.24%. Considerable fluctuations in soil temperature and air temperature near the ground (Fig. 1). Sands strongly eroded by wind.

Stand 2. Patch of *Spergulo-Corynephoretum* association situated in a local depression in the area. Density of plant cover – 40%. Number of individuals of *Spergula vernalis* per 1 m^2 – 269. A layer of fossil humus is faintly visible in the soil profile. Soil moister than on stand 1, and richer in nutrient components. Sands strongly eroded by wind.

Stand 3. Patch of *Spergulo-Corynephoretum* association in optimum phase. Large percentage of *Polytrichum piliferum* Schreb. (60%). Number of individuals of *Spergula vernalis* per 1 m^2 – 194. Soil profile weakly formed. Humus content at depth of 10 cm – 0.38%. Lesser fluctuations in soil and air temperature than on stand 1 (Fig. 1).

Stand 4. Patch of Arctostaphyllo-Callunetum association, density of vascular cover – 75%, considerable percentage of Cladonia rangiferina (L.) Web. Number of individuals of *Spergula vernalis* per 1 m^2 – 193. Distinct humus horizon in soil profile (6 cm); humus content at depth of 10 cm – 1.40%. Soil moister than on stands 1, 2, 3. The compact vegetation renders air and soil temperature milder (Fig. 1).

Stand 5. Patch of very dense grassy vegetation (95%), with *Calamagrostis epigeios* Roth. as dominating species. Number of individuals of *Spergula vernalis* per 1 m^2 – 93. Distinct (6–8 cm) humus horizon in soil profile. Soil dry but relatively rich in nutrient components. Air and soil temperatures similar to those on stand 4.

On account of the open character of the area, unshaded by tree stands, such elements of the climate as insolation and cloudiness have been omitted from the elaboration; detailed climatic data refer only to air temperature (extreme and mean daily temperatures) and daily total of rainfall during the period of growth and development of *Spergula vernalis*, omitting the resting stage of the seeds in the soil and winter resting stage of the first whorl. These data are given in diagrams (Fig. 2, 3).

3. DISCUSSION OF RESULTS

3.1. General course of phenophases in relation to climatic conditions

The phenological spectra (Fig. 4, 5, 6) included in this paper point to certain differences in the development of *Spergula vernalis* during the three-year observation period, in respect both of the length of the whole vegetative cycle and the various phenophases. There appears to be no doubt about the effect of temperature and precipitation on the times of certain phenophases. These factors act jointly or, in a given stage, only one of them plays a dominating role.

The effect of rainfall is very marked during the germination period, differences in the time of germination being as much as two weeks in extreme cases. Seedlings appeared

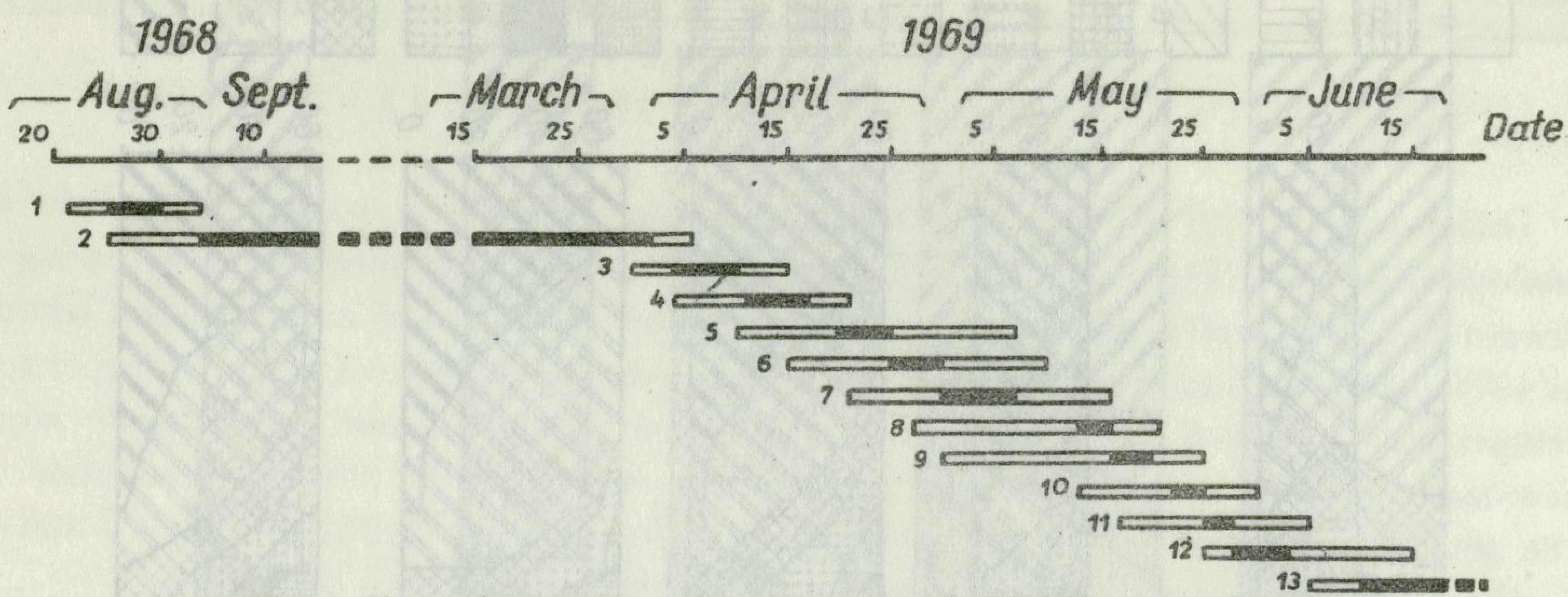

Fig. 4. Phenophases of *Spergula vernalis* in 1968/1969 on stand 2

1 – seedling, *2* – one leaf whorl, *3* – two leaf whorls, *4* – three leaf whorls, *5* – inflorescence buds, *6* – flower buds, *7* – early stage of blooming, *8* – full blooming, *9* – end of blooming, *10* – first immature fruits, *11* – full fructification, *12* – mature fruits and dissemination of seeds, *13* – drying up of plants

Shaded fields indicate period of phase domination

latest in 1970, probably as the result of the unfavourable distribution and small total amount of rainfall in August of that year.

The phases of winter rest of the plant, in the form of a short stem with only one leaf whorl, last for a long time. Further development depends on when the snow cover disappears and on air temperature. The number of individuals forming a second leaf whorl under the snow is negligible, and therefore generally speaking their development can be considered as a symptom of the end of the winter rest period. The time of this phenophase is in no way connected with the time at which seeds germinate (cf. spectra), but is clearly correlated with climatic conditions.

The subsequent stages of development usually last a short time only and the dates of consecutive phenophases in the study years compared are very similar, despite differences in air temperature and rainfall (Fig. 2, 3, 5, 6). The almost simultaneous time of flowering of the plants (i.e., in the majority of individuals) suggests that unlike the early stages, the influence of the autorhythmicity of the species predominates over the effect of habitat factors understood in a wide sense.

Maturation and dissemination of seeds and drying up of stems and leaves took place most abruptly in 1971, which in view of the abundant rainfall accompanying these phases would appear unjustified but in fact – after Newman (1965) – the ageing rate of plants is conditioned by drought, however short-lived, during the formation of the flowers, and therefore during the period preceding the terminal stages of life. Analysis of precipitation in April and May on the one hand, and the course of the final phenophases in the study years on the other hand, completely confirm Newman's (1965) view.

When the curve of survivorship (upper line of spectrum – Fig. 5, 6) is traced in relation to the successive phases of the plant development, the conclusion is reached that maximum mortality is found in the one leaf whorl stage. This phenomenon can be interpreted in two ways: (a) intensification of competition during the juvenile age of plants (Zarzycki 1965) and (b) effect of unfavourable external conditions in winter. The exceptionally long and hard winter in 1969/70 most certainly contributed to the greater disappearance of individuals than in the other years.

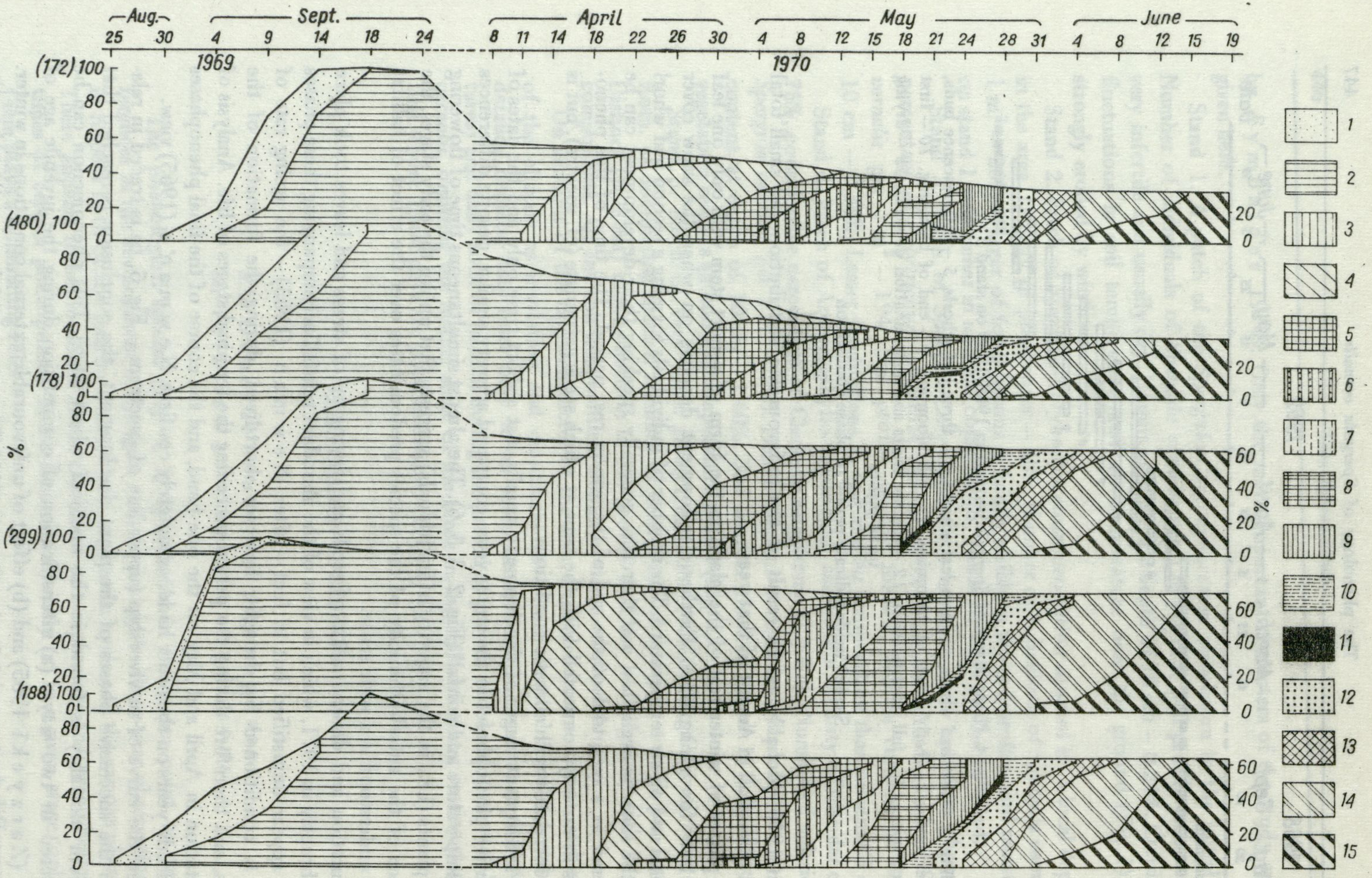

Fig. 5. Phenological spectrum of five populations (1969/1970)

Phases *1–15* explained in text (Section 2)

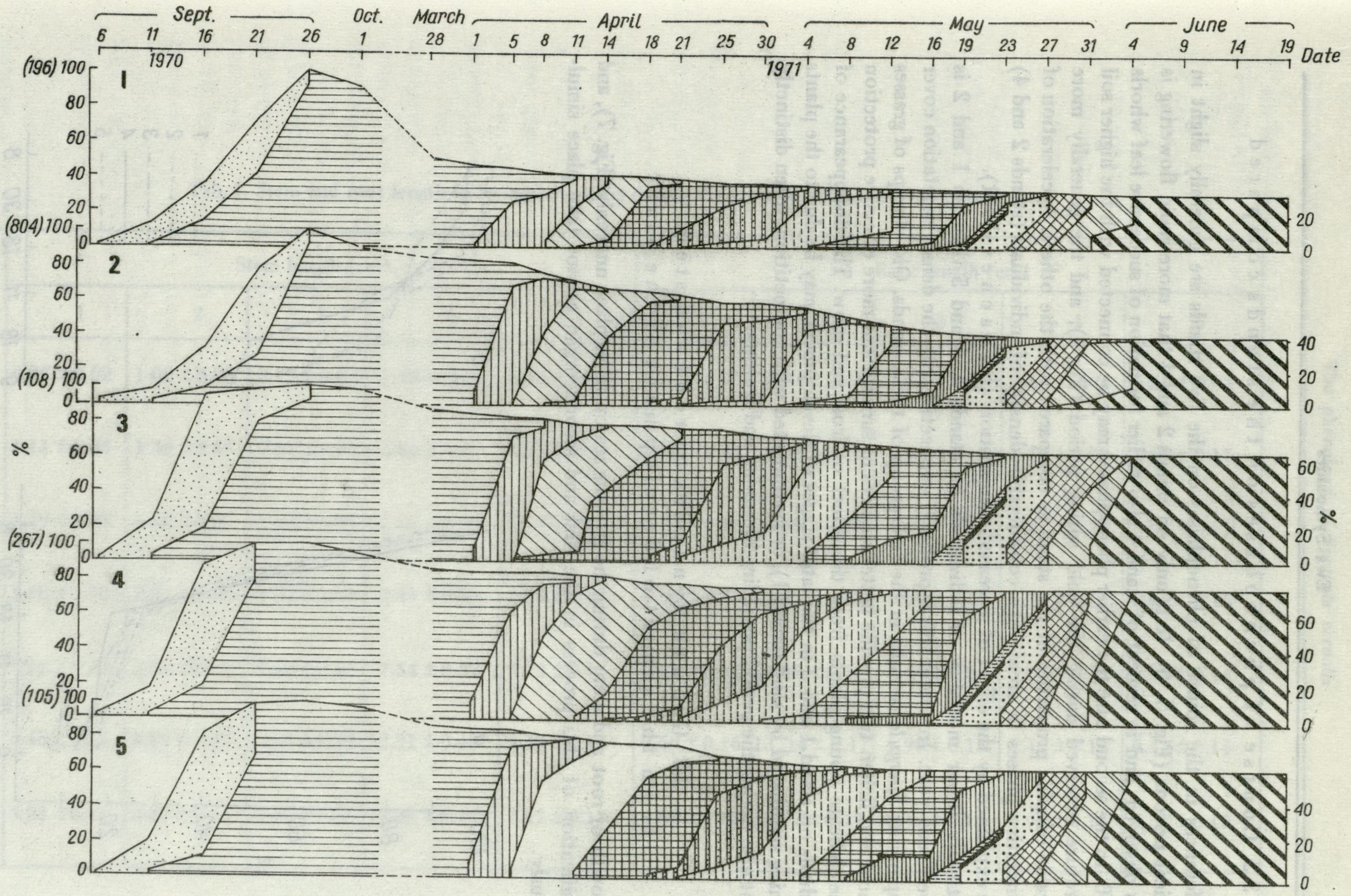

Fig. 6. Phenological spectrum of five populations (1970/1971)

Symbols of phases as in Figure 5

3.2. Course of phenophases on the stands compared

Differences in the course of phenophases on the five stands are generally slight in analogical periods (Fig. 5, 6). It is only on stands 2 and 4 that more rapid flowering is always observed, and in respect of stand 4 also earlier formation of successive leaf whorls in 1970. In the second case the earlier phenophases may be connected with the higher soil temperature observed during the cold spring period (Fig. 1), and the generally more favourable edaphic properties of the stand as compared with the others. Acceleration of the generative phases in areas with considerable density of individuals (stands 2 and 4) can be explained by the effect of increased competition (Sukachev 1941).

Distinctly lower mortality of individuals on stands 3, 4 and 5 than on 1 and 2 is observed each year. In winter this is probably connected with the denser vegetation cover accompanying *Spergula vernalis* in the first group of these stands. Old clumps of grasses and moss and lichen turf provide better chances of survival and more effective protection for the delicate young plants from the effect of frost and snow. The disappearance of individuals on stand 1 and 2 in the later stages of development may be due to the plants becoming smothered by sand (stand 1), or is connected with competition, often distinctly evident also during the period proceding blooming and fruiting.

3.3. Growth dynamics of root and stem from the aspect of development of the plant

Growth of root and stem during the growing season takes place unevenly (Fig. 7), and intensification of this process in the first and second organ cannot take place simultaneously.

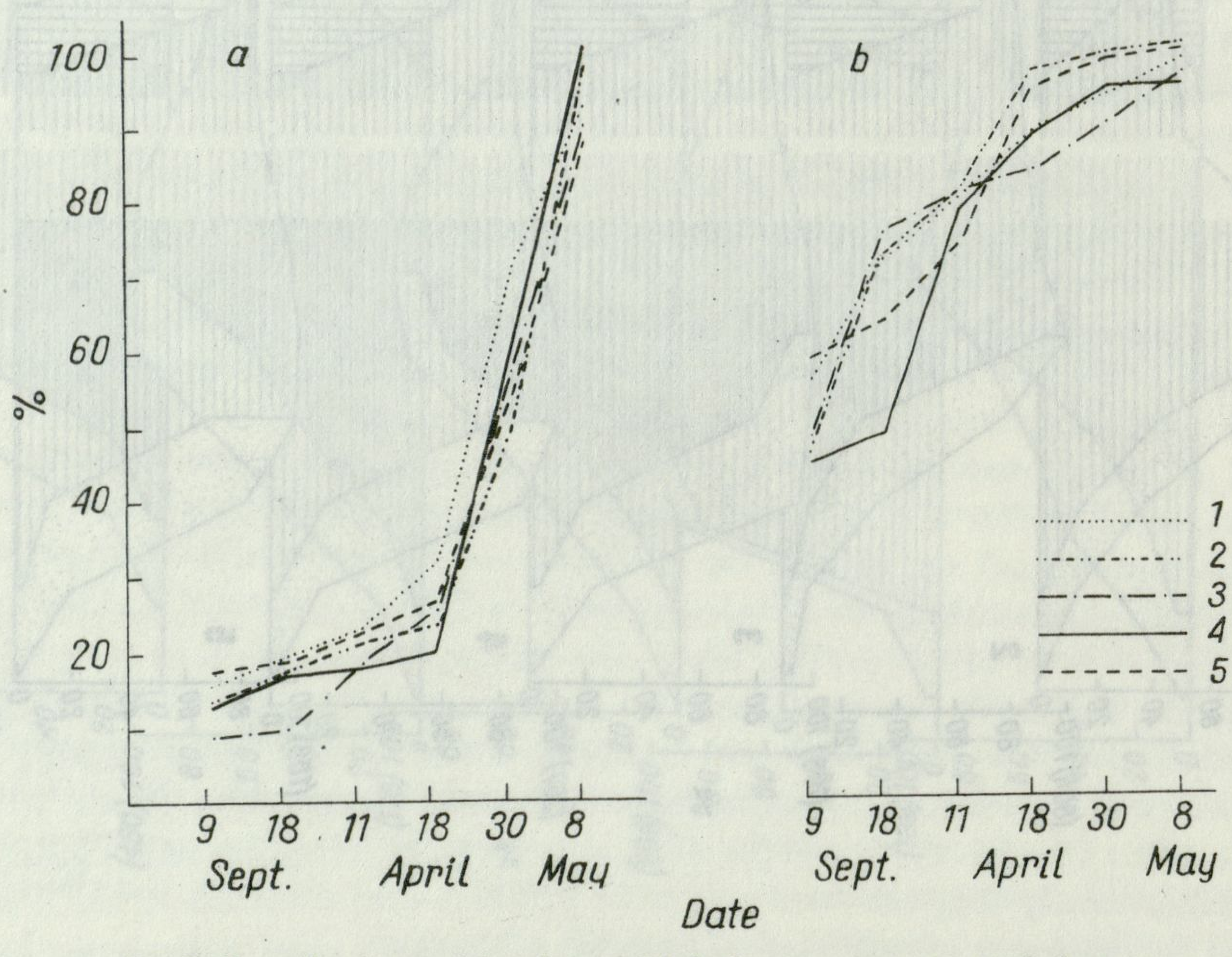

Fig. 7. Growth of stem *(a)* and root *(b)* during growing season of plant

Final length of stem and root taken as 100%, *1–5* – populations

Tab. I. Stem and root length in *Spergula vernalis* during the growing season (1–5 – populations)

Date	Stem length (cm)					Root length (cm)				
	1	2	3	4	5	1	2	3	4	5
9 Sept. 1969	0.87 ± 0.02	1.00 ± 0.06	0.77 ± 0.02	1.49 ± 0.04	1.16 ± 0.03	5.41 ± 0.07	5.74 ± 0.04	4.94 ± 0.06	3.46 ± 0.05	5.53 ± 0.03
18 Sept. 1969	1.11 ± 0.05	1.36 ± 0.05	0.81 ± 0.04	2.00 ± 0.06	1.28 ± 0.03	6.96 ± 0.13	9.34 ± 0.15	7.82 ± 0.14	3.78 ± 0.08	5.98 ± 0.17
11 April 1970	1.29 ± 0.03	1.66 ± 0.05	1.59 ± 0.05	2.12 ± 0.07	1.52 ± 0.03	7.77 ± 0.14	10.40 ± 0.15	8.37 ± 0.12	6.12 ± 0.22	6.96 ± 0.17
18 April 1970	1.80 ± 0.06	1.86 ± 0.08	2.32 ± 0.06	2.49 ± 0.03	1.82 ± 0.07	8.60 ± 0.14	12.57 ± 0.16	8.69 ± 0.14	6.94 ± 0.19	8.92 ± 0.16
30 April 1970	4.12 ± 0.12	4.09 ± 0.12	5.30 ± 0.14	7.54 ± 0.22	3.73 ± 0.12	9.15 ± 0.14	12.88 ± 0.16	9.29 ± 0.13	7.45 ± 0.15	9.30 ± 0.14
8 May 1970	5.45 ± 0.14	8.09 ± 0.15	8.43 ± 0.29	12.91 ± 0.40	6.18 ± 0.12	9.59 ± 0.16	13. 14 ± 0.17	9.98 ± 0.15	7.40 ± 0.14	9.43 ± 0.14
18 May 1970	5.93 ± 0.11	8.29 ± 0.15	9.43 ± 0.25	12.94 ± 0.35	7.17 ± 0.13	9.84 ± 0.15	13.17 ± 0.17	10.48 ± 0.14	7.94 ± 0.15	9.54 ± 0.15

Growth of the root is particularly intensive in the early stages of development of the plant (cf. S t r u i k 1965), as is shown by the results of measurements made on 18 September (Tab. I), when the roots had attained almost half (on stand 4) or more than half (on the remaining stands) of their normal length. The weaker growth of roots in the later stages may be due to the inhibiting influence, which is particularly intensive at that time, of the growth of the upper parts of plants (K o t a ń s k a 1970). The results suggest that root growth also takes place in winter, although very distinct differences in measurements made in spring and autumn apply only to individuals from stand 4. Slow and gradual growth of roots in winter was observed in his studies by T r o u g h t o n (1951).

Stem growth, at first minimal, is most clearly evident during the period directly preceding blooming, after which period it again decreases. The rate of stem growth (and also root growth), expressed in percentages of final length, is in all cases similar on the

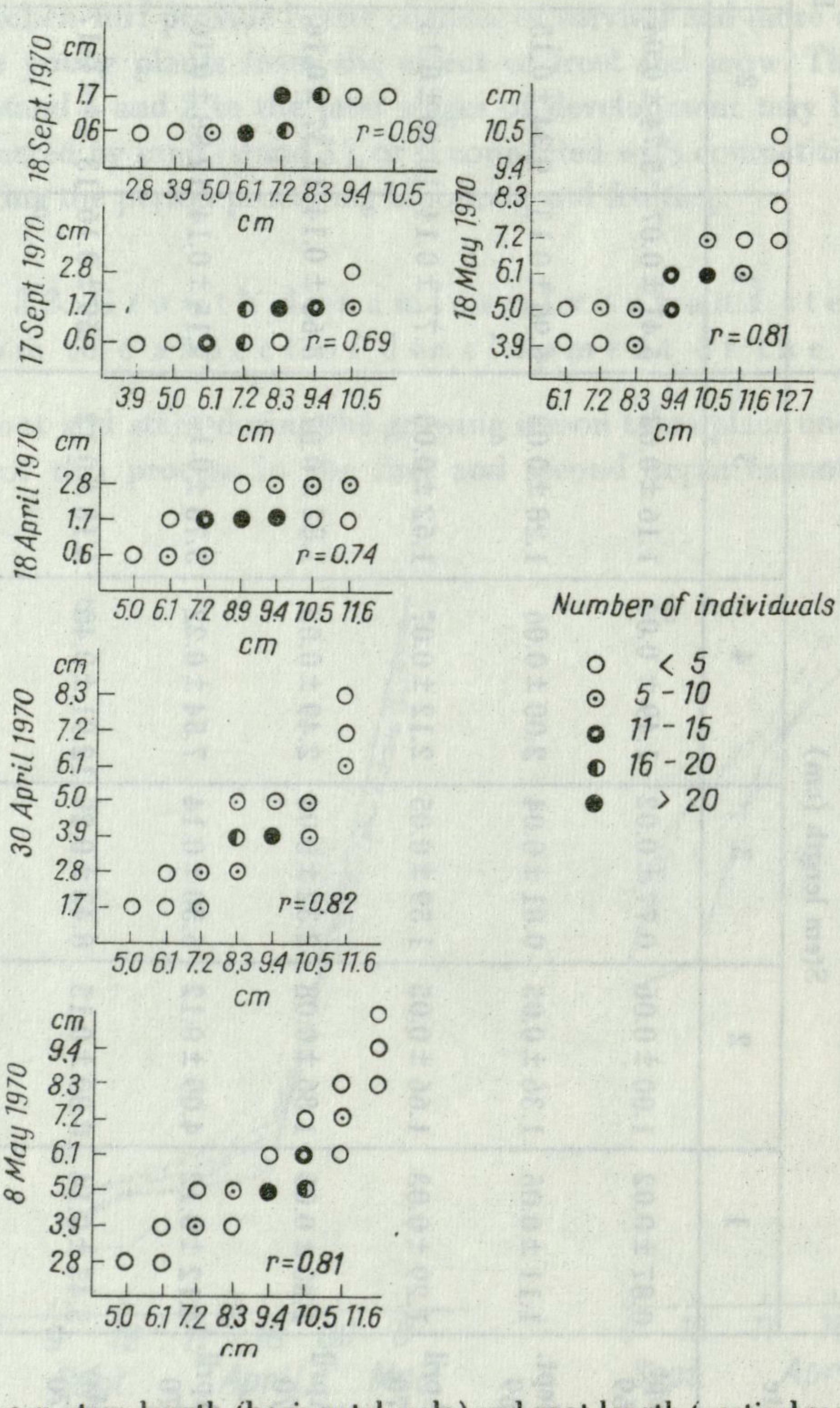

Fig. 8. Relation between stem length (horizontal scale) and root length (vertical scale) during growing season of *Spergula vernalis* (population 1)

study stands (Fig. 7), the differences found applying only to absolute length of these organs (cf. Tab. I and S y m o n i d e s 1974b).

Stem length is positively correlated with root length over the whole life cycle of *Spergula vernalis*, the correlation of the two organs increasing as the plant matures (Fig. 8). This regularity was found in all the populations.

4. CONCLUSIONS

1. The ability of *Spergula vernalis* to grow over outstandingly dry sands is due to its short life cycle, limited to the autumn and spring periods, when the soils are relatively well supplied with water.

2. The length of the whole cycle, and also some of the phenophases, depend on air temperature and precipitation. The influence of precipitation primarily affects the date on which seeds germinate; during a period of drought the seeds germinate about 2 weeks later than is the case during rainy weather.

3. The period of the plant's winter rest is synchronized with the duration of snow cover and air temperature.

4. The time at which *Spergula vernalis* blooms is regulated by the autorhythmicity of the species. It does not exhibit connection with the date of seed germination or with climatic conditions.

5. The rate at which the plants age is conditioned by drought during the period when the flowers form, that is, during the period preceding the terminal stages of life.

6. With high population density, that is, under conditions of intensified competition, a certain degree of acceleration of the generative phases takes place in relation to the less dense populations.

7. The higher soil temperature and the greater resources of nutrient components of the biotope cause acceleration of the majority of the phenophases.

8. Maximal mortality is characteristic of the early stages of the plant's life in the ontogenesis of *Spergula vernalis*. The survival of individuals is, in general, lower in the areas covered by sparse vegetation, as the harmful effect of frost and snow in winter and the destructive effect of windborne sand in the late spring are particularly marked there.

9. The most intensive growth of roots takes place during the juvenile period of *Spergula vernalis*; it is also evident to a minimum degree in winter. Growth of the upper parts of plants takes place most abruptly in spring during the period immediately preceding blooming.

10. The rate of growth of stem and root is similar on all the biotopes; differences are found only in respect of the absolute length of the two organs.

11. Throughout the whole ontogenesis of *Spergula vernalis* stem and root length exhibit a distinct positive correlation; the degree of this correlation increases with the development of the plant.

My grateful thanks are due to Professor Dr. K. Zarzycki for his help and guidance during the execution of this study.

5. SUMMARY

The development rhythm of an ephemeral dune species, *Spergula vernalis* Willd. was traced over the course of three growing seasons in relation to air temperature and precipitation. Fifteen phenophases were taken into account. Observations were made every 3–5 days from 1968 to 1971 in five different dune biotopes in the Toruń Basin.

The results are presented in the form of spectra on which succession of phenophases, their duration, exact quantitative relations of individuals present in different phases and also the capacity for survival of individuals are indicated.

Phenological observations were supplemented by phenometrical measurements of root and stem and calculation of the coefficient of correlation between these organs during the growing season of *Spergula vernalis*.

The following conclusions can be drawn on the basis of the observations and measurements made:

1. The early development phases of *Spergula vernalis*, in particular germination of seeds and the phase of one leaf whorl, are distinctly synchronized with atmospheric precipitation and air temperature. The duration of the whole growing cycle of this plant depends on the time the seeds germinate (Fig. 4, 5, 6).
2. After the period of winter rest until the time the plants bloom inclusively the predominance of the autorhythmicity of the species over the influence of habitat factors is very distinct. Despite the different climatic conditions in the years compared the plants were observed to bloom almost at the same time.
3. The ageing rate of plants is conditioned by drought during the period when the flowers form, that is, the period preceding the final stages of the plant's life.
4. The phenomenon of acceleration of the majority of the phenophases in relation to outstandingly infertile biotopes can be seen in biotopes richer in nutrient components and characterized by higher soil temperature (stand 4).
5. With high population density, with consequent increased competition (stands 2, 4), some degree of acceleration of the generative phases was observed in comparison with less dense populations.
6. During the development cycle of *Spergula vernalis* maximal mortality is found during the juvenile stages of the plant, the number of individuals dying depending on the character of the biotope. On areas scantily covered by vegetation the harmful effect of frost and snow in winter, and also the destructive effect of windborne sand in late spring, are more strongly marked.
7. While the most intensive growth of the root takes place during the juvenile age of *Spergula vernalis*, the growth of the upper parts of the plant takes place during the period immediately preceding blooming (Fig. 7). Rate of growth of stems and roots is similar on all the stands.
8. Length of stem and root are always characterized by positive correlation, the degree of this correlation increasing with the development of the plant (Fig. 8).
9. The short life cycle of *Spergula vernalis*, limited to the period of autumn and spring, when the soils are relatively well supplied with water, makes it possible for this plant to occupy outstandingly dry, infertile sands and constitutes the plant's basic adaptation to the specific conditions prevailing on dunes.

6. POLISH SUMMARY (STRESZCZENIE)

W ciągu trzech sezonów wegetacyjnych prześledzono rytmikę rozwojową efemerycznego gatunku wydmowego *Spergula vernalis* Willd. na tle temperatury powietrza i opadów. W obserwacjach uwzględniono 15 faz fenologicznych. Przeprowadzono je co 3–5 dni w latach 1968–1971, na pięciu różnych siedliskach wydmowych Kotliny Toruńskiej.

Wyniki zestawiono w postaci spektrów, na których zaznaczone są następstwa pojawów, czas ich trwania, dokładne stosunki ilościowe osobników znajdujących się w różnych fazach a także przeżywalność osobników.

Obserwacje fenologiczne uzupełniono pomiarami fenometrycznymi korzenia i łodygi oraz obliczeniem współczynników korelacji między tymi organami w sezonie wegetacyjnym *Spergula vernalis*.

W wyniku przeprowadzonych obserwacji i pomiarów można wyprowadzić następujące wnioski:

1. Wczesne fazy rozwojowe *Spergula vernalis*, zwłaszcza kiełkowanie nasion i faza jednego okółka liści, są wyraźnie zsynchronizowane z opadem atmosferycznym oraz temperaturą powietrza. Od terminu kiełkowania nasion uzależniony jest czas trwania całego cyklu wegetacyjnego badanej rośliny (fig. 4, 5, 6).

2. Po okresie zimowego spoczynku rośliny do kwitnienia włącznie zaznacza się przewaga wpływu wewnętrznej rytmiki gatunku nad działaniem czynników środowiskowych. Pomimo różnych warunków klimatycznych w porównywanych latach, obserwowano prawie równoczesny moment zakwitania roślin.

3. Tempo starzenia się roślin uwarunkowane jest suszą w okresie tworzenia się kwiatów, a zatem w okresie wyprzedzającym końcowe stadia życia.

4. Na siedliskach zasobniejszych w składniki pokarmowe, charakteryzujących się przy tym wyższą temperaturą gleby (stanowisko 4), występuje zjawisko przyspieszenia większości pojawów fenologicznych, w stosunku do siedlisk wybitnie jałowych.

5. Przy dużym zagęszczeniu populacji, w warunkach zwiększonej konkurencji (stanowiska 2, 4), obserwowano pewne przyspieszenie faz generatywnych w porównaniu z populacjami słabiej zwartymi.

6. W cyklu rozwojowym *Spergula vernalis* najwyższa śmiertelność charakteryzuje stadia młodociane rośliny, przy czym liczba ginących osobników uzależniona jest od charakteru siedliska. Na powierzchniach skąpo pokrytych roslinnością silniej zaznacza się zarówno szkodliwy wpływ mrozu i śniegu zimą, jak też niszczące działanie lotnego piasku w okresie późnej wiosny.

7. O ile najintensywniejszy wzrost korzenia następuje w wieku młodocianym *Spergula vernalis*, o tyle wzrost części nadziemnych – w okresie bezpośrednio poprzedzającym kwitnienie (fig. 7). Tempo wzrostu łodygi i korzenia jest podobne na wszystkich siedliskach.

8. Długość łodygi i długość korzenia cechuje zawsze współzależność dodatnia, przy czym stopień tej współzależności wzrasta wraz z rozwojem rośliny (fig. 8).

9. Krótki cykl życiowy *Spergula vernalis*, ograniczony do okresu jesieni i wiosny, kiedy gleby są stosunkowo dobrze zaopatrzone w wodę, umożliwia jej zajmowanie wybitnie suchych, jałowych piasków i stanowi podstawową adaptację rośliny do specyficznych warunków panujących na wydmie.

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