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EFECT OF POPULATION DENSITY ON THE PHENOLOGICAL DEVELOPMENT OF INDIVIDUALS OF ANNUAL PLANT SPECIES

ABSTRACT: During a six years' period the course of the life cycle was observed of five species of dune annuals at three different density levels. The studies have shown that: (1) the time of seedling emergence and the duration of the seedling phase depend primarily on the weather conditions; (2) after the seedling phase has been passed, an increase in density is accompanied by an acceleration of the developmental phases (until the flowering time) and shortening of the life cycle; (3) the shorter the growth cycle of a species the more marked is the effect of density on the phenological development of individuals.

KEY WORDS: Psammophytes, therophytes, population density, phenological development of annuals, developmental rhythmicity of annuals, duration of phenophases.

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1. INTRODUCTION

Many studies concerned with the effect of the density of a population on its other properties, as well as on the characteristics of the individuals, were focused primarily on the problems of an increases mortality under the conditions of an intensified competition as a result of overcrowding (Marschall and Jain 1969, 1970, Mathews and Westlake 1969, Ross and Harper 1972, Symonides 1974, 1977, and many others). There have also been many papers dealing with the relationship between the density of individuals and their size and weight (Palmblad 1968, Putwain and Harper 1970, White and

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Harper 1970, Symonides 1974), between the density and the percentage of flowering and fruiting individuals in a population (Rabotnov 1950, Harper and Ogden 1970), production of fruit and seeds and their germinating capacity (Salisbury 1942, Knapp 1954, Zarzycki 1965).

The studies have revealed that population density also affects the development rate of plants and their phenology. The most frequent result of the phenological reaction of plants to overcrowding is an elongation of the life cycle and retardation of the successive phenophases. This applies primarily to all biennial and perennial species (Linkola 1935, Rabotnov 1950, Palmblad 1968). A reverse phenomenon, i.e., an accelerated development under the conditions of a high density has been observed among the annuals (Sukačev 1941, Palmblad 1968, Wilkoń-Michalska 1976).

However, the phenological reaction of plants to population density has not so far been the object of separate studies which would compare the dates and the course of the successive phenophases, and the phenological differences among individuals within a population at different densities. This problem was the object of the investigations presented in this paper dealing with annual psammophyte species. The paper is part of a wide-scope series of studies of the phenology of dune plants, taking into account biennial and perennial species.

2. STUDY AIMS AND METHODS

The observations were carried out, in the years 1968–1973, in four different plant communities on the dunes of the Toruń Basin. The general description of the study area, the soils, climate and vegetation can be found in the paper by Symonides (1974). The weather conditions during the study period have been presented by means of Walter's (1962) climatic diagrams, prepared on the basis of the data obtained from the Toruń-Wrzosy Station of the Institute of Meteorology and Water Management (Fig. 1).

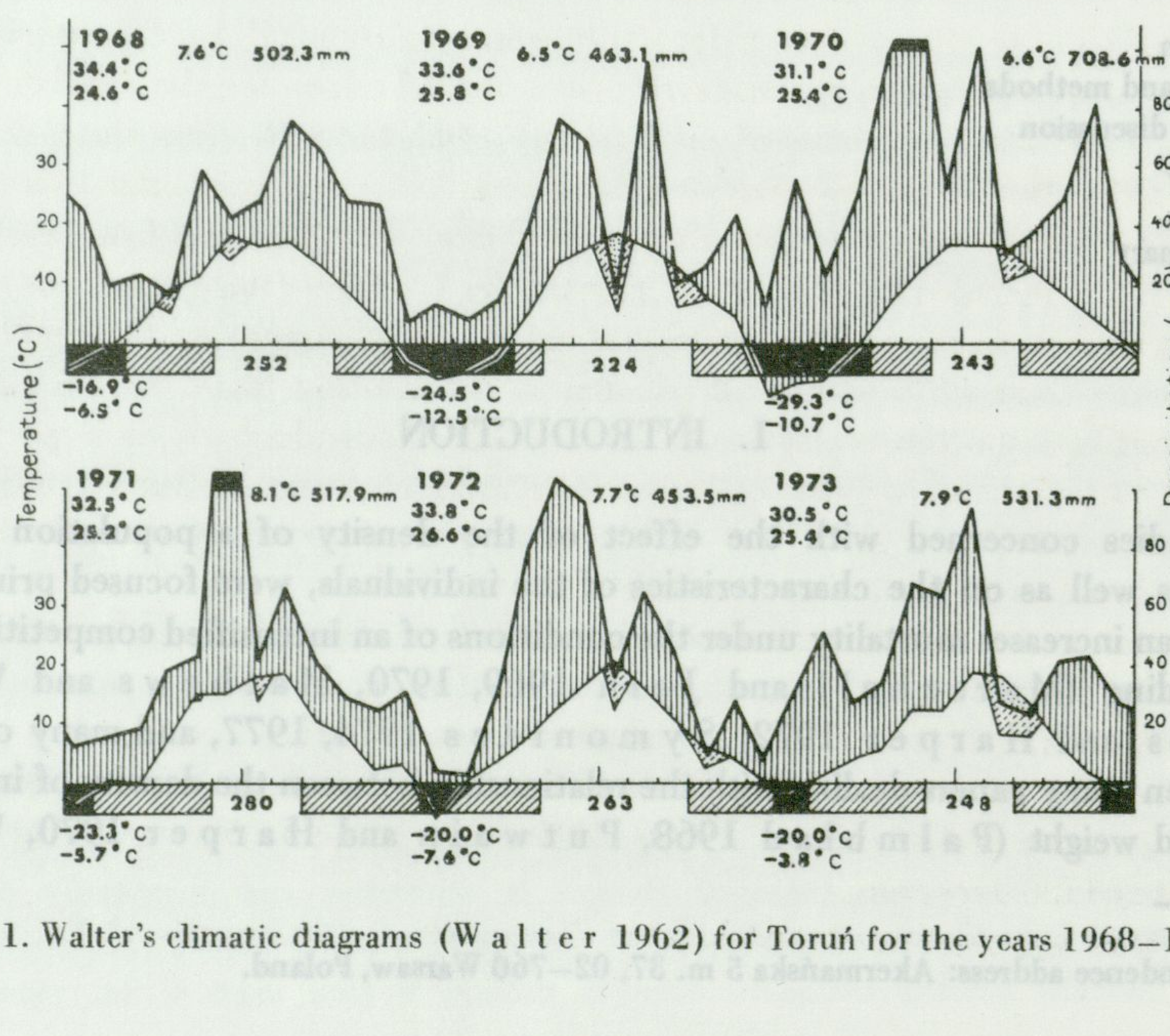

Fig. 1. Walter's climatic diagrams (Walter 1962) for Toruń for the years 1968–1973

The plant species, selected for the studies, differed in respect of both the total duration of the developmental cycle and the dates and the course of the successive phenophases. Listed in order of increasing life span they were as follows: *Cerastium semidecandrum* L. – most often germinating as early as the end of the calendar winter, *Androsace septentrionalis* L. – with its developmental cycle being completed during the spring, *Plantago indica* L. – germinating in spring and flowering in summer, *Trifolium arvense* L. – germinating, like the former species, in spring, but with a very long flowering period, until early autumn, and *Spergula vernalis* Willd. – a species that winters in the seedling stage and flowers in the spring of the following year.

On the basis of the preliminary analysis of the developmental rhythmicity of the species under study during the first study year the frequency of observations was established, as well as the phases which were subsequently used for determining the developmental stages of the individuals: (1) seedling phase, (2) growing phase, (3) inflorescence bud phase (this did not apply to *Cerastium semidecandrum*), (4) flower bud phase, (5) flowering phase, (6) unripe fruit phase, (7) phase of ripe fruit and seed dissemination, (8) dying phase. Where in the same plant several phenophases could be seen simultaneously (e.g., flower buds, fully developed flowers with unripe seeds occurred simultaneously in one individual), the feature taken into account was the time of dominance of a phase.

In the detailed phenological observations carried out every 3–5 days, depending on the intensity of the phenomena, in the years 1969–1973 the numeric ratios between individuals in different developmental stages were considered. The observations were conducted in five permanent areas, each of the size 2×4 m, divided into 400 equal-sized plots; thus the area of one plot was $0.02\ m^2$. On the day of observation, in each of the plots the total number of individuals per a developmental phase was recorded.

Because the main objective of the study was to demonstrate any possible relationships between the rate of development and density, the results have been worked out on the basis of the data from specially selected plots representing (in equal numbers) three classes of density of individuals of the same species. The selection of the plots was based on the following method: (1) all plots in which individuals of other species, of one or more (except single specimens) occurred in addition to the species under study were excluded; (2) for the remaining plots five density classes were established (considering the range of values for the number of individuals determined for the seedling phase of each species) and for each class the mean density was calculated; (3) for the statistical analysis of the results for the particular year 30 plots, with densities nearest to the mean density of a given class, were selected from each of the total numbers of plots included in the lowest (first), the medium (third) and the highest (fifth) density classes; the remaining plots were not taken into account. In the seedling phase the density ratio for these plots was 1 : 2 : 4, and in the fruiting phase 1 : 1.5 : 2. The average number of seedlings and the average number of fruiting individuals of each species in a plot in two different years have been given, only as examples, in Figures 2–6 further on in the text.

In the comparative analysis of the developmental rhythmicity of the species under study with varying densities the following were taken into account:

1. total duration of the life cycle, from the emergence of the first seedlings to the death of a half of the population;

2. duration of each of the developmental phases;

3. the time of maximum intensity of the phases of flower buds, of flowering, of ripe fruit, of seed dissemination and of dying – relative to the date of the occurrence of first seedlings;

4. the date of full flowering.

The statistical hypotheses on the lack of differences in the length of the whole developmental cycle, of the individual phenophases and in the time of the maximum intensity of selected developmental phases at different densities and in different years have been verified by the test of double analysis of variance (G r e ń 1974), using square root transformation of the empirical data. Where differences were found at the significance level of 0.05, Duncan's multiple range test (O k t a b a 1966) was used, and correlation coefficients were calculated to find out how and to what extent density affects the development of the species studied.

3. RESULTS AND DISCUSSION

The course of the individual phenophases of the species under study, in the years that differed most in respect of the date of the first germs has been presented in the phenological spectra (Figs. 2–6), drawn by B e i d e m a n ' s (1954) method, with data for high, medium and low densities given separately. The spectrum scale is comparable, because 100% is always represented by the total number of individuals in all the plots analysed jointly, because of their

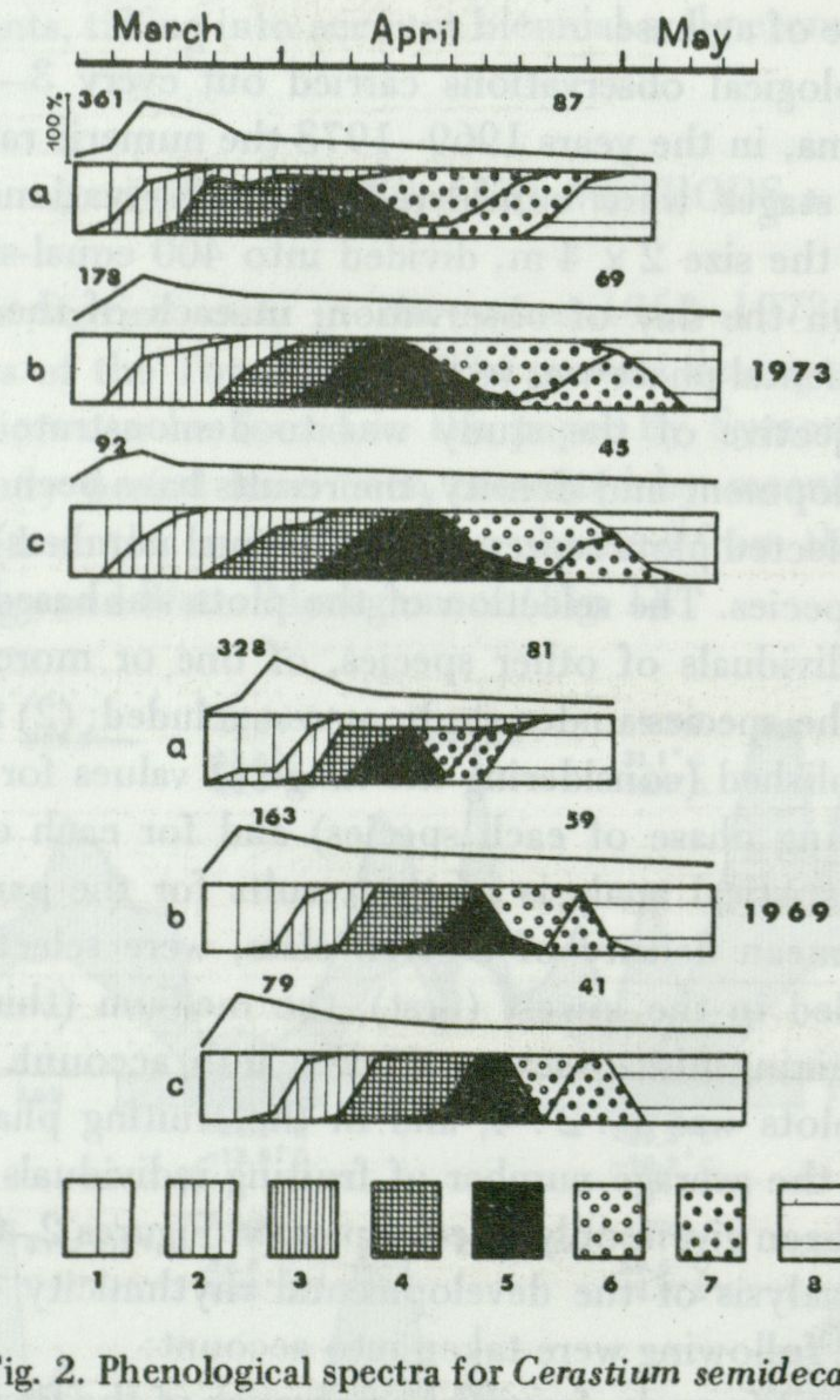

Fig. 2. Phenological spectra for *Cerastium semidecandrum*

Phenophases: 1 – seedling, 2 – growing stage, 3 – inflorescence buds (applies to the remaining species, see Figs. 3–6 – there are no inflorescence buds in *C. semidecandrum*), 4 – flower buds, 5 – flowering, 6 – unripe fruits, 7 – ripe fruits and seed dissemination, 8 – dying of plants. Densities: a – high, b – medium, c – low. The curve above the spectrum represents the percentage of individuals that emerged and of those that survived, relative to the total number of seedlings ; the numbers given above the spectrum denote the average density of individuals per plot in the seedling phase (left) and in the phase of ripe fruits and seed dissemination (right)

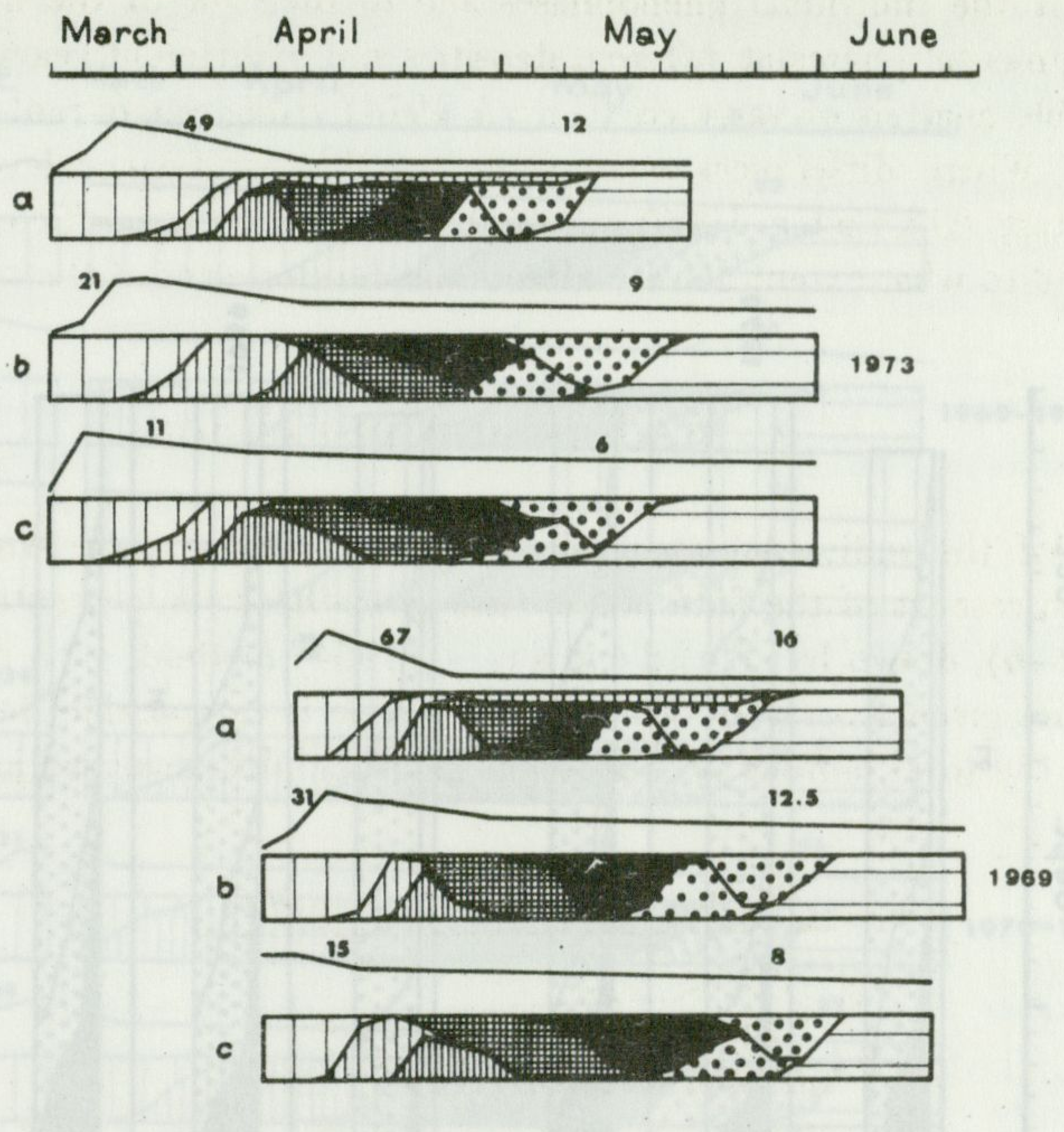

Fig. 3. Phenological spectra for *Androsace septentrionalis*
For explanations see Figure 2

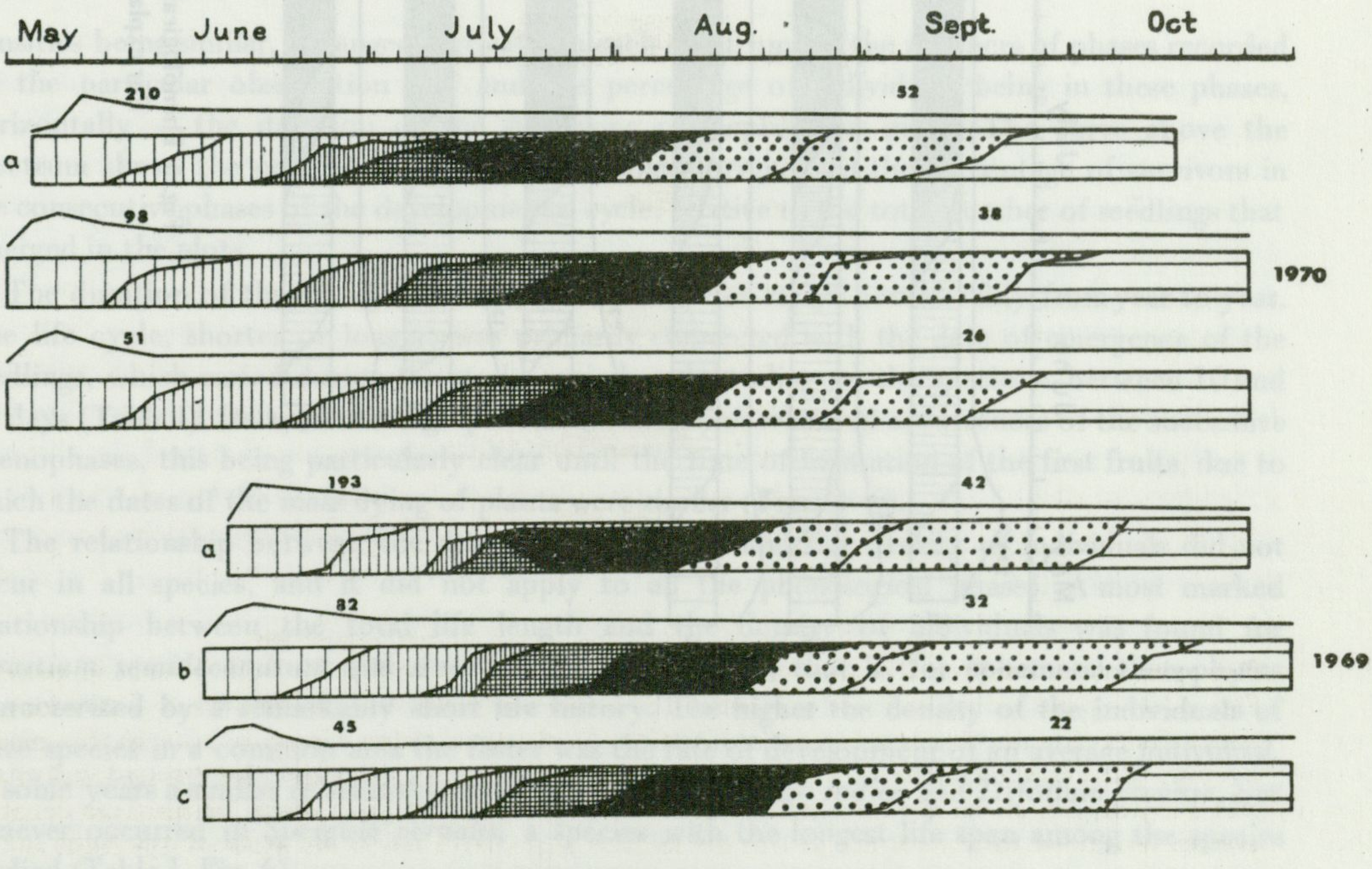

Fig. 4. Phenological spectra for *Plantago indica*
For explanations see Figure 2

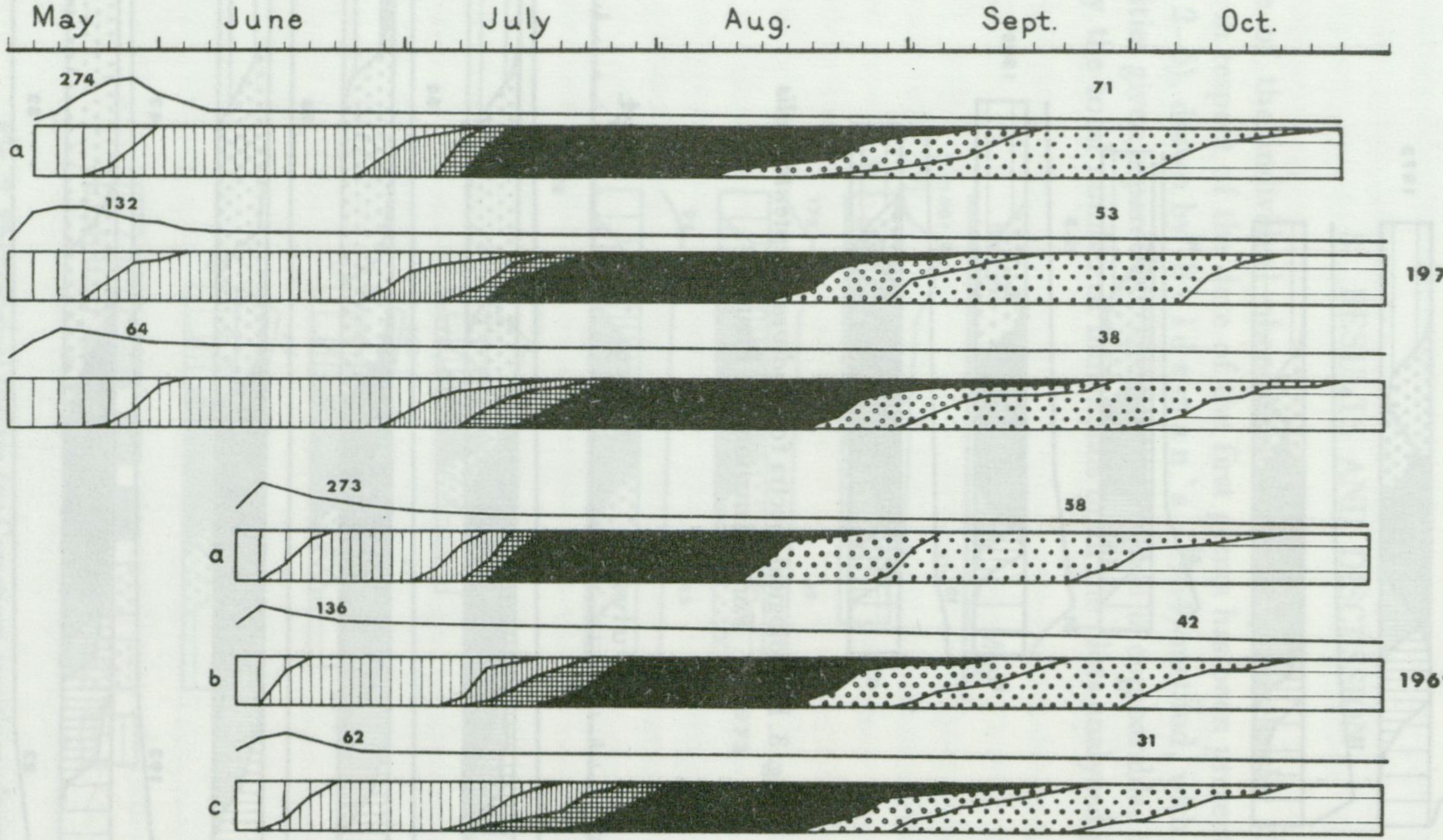

Fig. 5. Phenological spectra for *Trifolium arvense*
For explanations see Figure 2

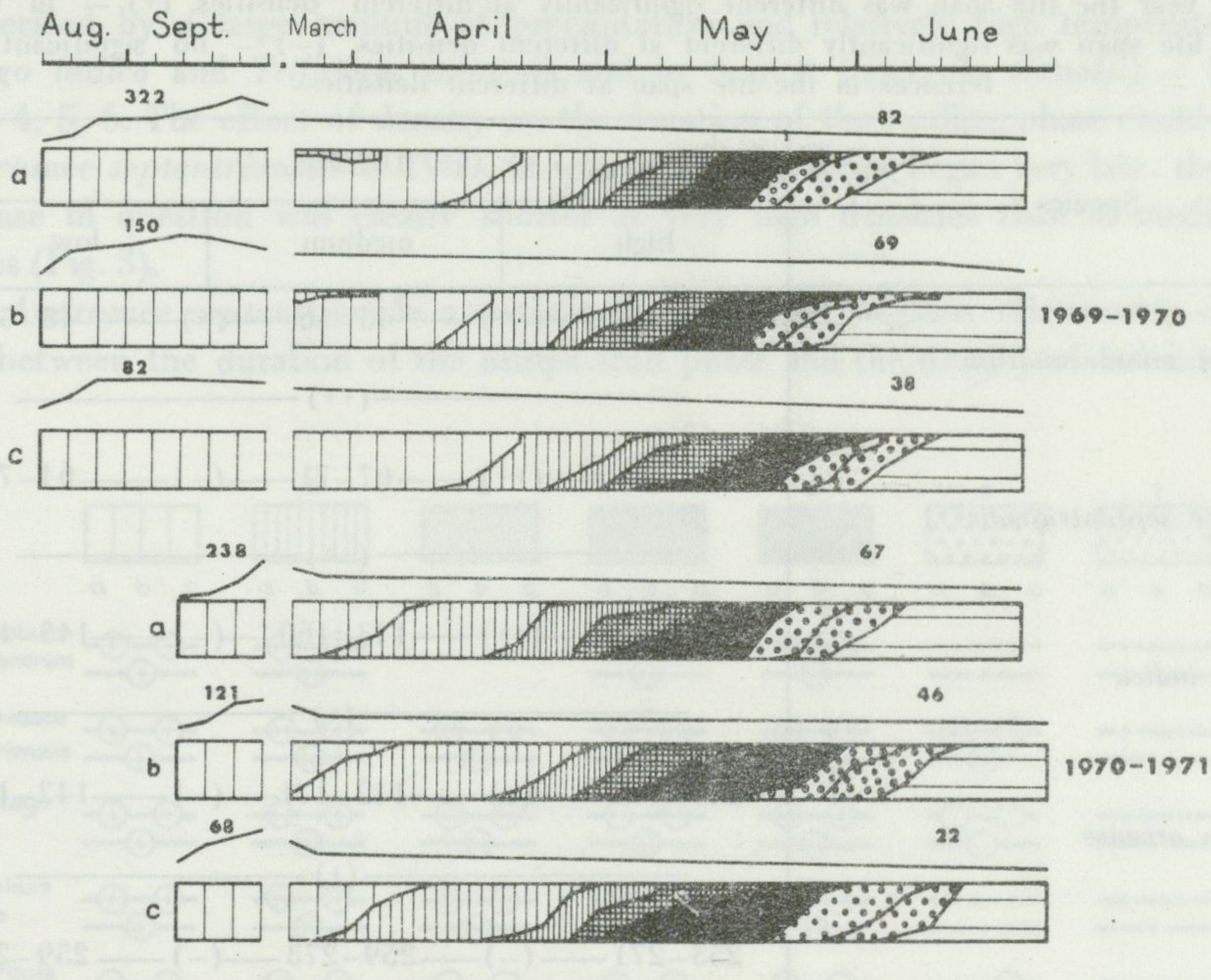

Fig. 6. Phenological spectra for *Spergula vernalis*
For explanations see Figure 2

densities being similar. Arranged vertically in each spectrum are the numbers of phases recorded on the particular observation day and the percentage of individuals being in these phases, horizontally – the duration of the successive phenophases is given. The curve above the spectrum shows the percentage of individuals that emerged and the percentage of survivors in the consecutive phases of the developmental cycle, relative to the total number of seedlings that emerged in the plots.

The duration of the life cycle of the selected species varied considerably from year to year. The life cycle, shorter or longer, was primarily connected with the date of emergence of the seedlings, which varied during the study period – depending on the species – between 10 and 27 days (Table I). Delayed coming up was followed by accelerated occurrences of the successive phenophases, this being particularly clear until the time of formation of the first fruits, due to which the dates of the mass dying of plants were similar (Figs. 2–6).

The relationship between the rate of development and the density of individuals did not occur in all species, and it did not apply to all the phenological phases. A most marked relationship between the total life length and the density of individuals was found for *Cerastium semidecandrum* and *Androsace septentrionalis*, that is, for ephemeral therophytes characterized by a remarkably short life history. The higher the density of the individuals of these species in a common area the faster was the rate of development of an average individual. In some years a similar relationship was recorded for *Plantago indica* and *Trifolium arvense*, but it never occurred in *Spergula vernalis*, a species with the longest life span among the species studied (Table I, Fig. 6).

Table I. Duration of life cycles (in days) of the species under study, at different densities (++) each year the life span was different significantly at different densities, (+) – in some years the life span was significantly different at different densities, (–) – no significant differences in the life span at different densities

Species	Density					
	high		medium		low	high – low
Cerastium semidecandrum	35–49	(++)	45–56	(+)	48–56	(++)
Androsace septentrionalis	55–60	(++)	67–71	(–)	64–71	(++)
Plantago indica	132–146	(++)	143–160	(–)	143–162	(+)
Trifolium arvense	139–162	(+)	142–171	(–)	142–173	(+)
Spergula vernalis	255–271	(–)	259–273	(–)	259–274	(–)

Under the conditions of a high density, an acceleration of the development is marked first of all in the growing phase and in the inflorescence bud, flower bud and flowering phases (Fig. 7). The duration of these phases was always significantly different in individuals which grew in different densities except *Spergula vernalis* for which only in certain years was a considerable relationship and negative value of the correlation coefficient found. However, it must be mentioned that in the estimation of the significance of the differences in the duration of analogous phenophases and in the calculation of the correlation coefficients for *Cerastium semidecandrum*, *Androsace septentrionalis* and *Plantago indica* several per cent of individuals have been left out. These were individuals whose development at a very high density had been impeded at the growing stage and they did not attain the generative phases of development (Figs. 2a, 3a, 4a). These individuals most often died before the mass dying of most of the individuals in the same plots. A protracted state of a certain "underdevelopment" is common in the perennials. (Rabotnov 1950).

In some years the individuals derived from different densities differed in the duration of the seedling phase; however, only in one case was a linear relationship found between the duration of this phase and density. Therefore the studies have not revealed any effect of density on the duration of the seedling phase, which, like the date of the emergence of the first seedlings, depends above all on the weather conditions (cf. Falińska 1973, Wilkoń-Michalska 1976). In the case of the ephemeral species of the early spring the beginning of the growing stage was associated with the date of disappearance of the snow cover (*Cerastium semidecandrum*) and of the ground frosts (*Androsace septentrionalis*) (cf. Fig. 1 and

Figs. 2, 3). For the remainder of the species an earlier germination occurred in years characterized by a large amount of precipitation and relatively high temperatures: in May (*Plantago indica* and *Trifolium arvense*) and in August (*Spergula vernalis*) – Figure 1 and Figures 4, 5, 6. The effect of density on the duration of the seedling phase could only be seen in *Androsace septentrionalis* in 1969, in which year the spring began very late: the duration of the phase in question was clearly shorter at very high densities than at medium and low densities (Fig. 3).

For *Androsace septentrionalis* a statistically significant, negative relationship could also be found between the duration of the unripe fruit phase and the density of individuals. For the

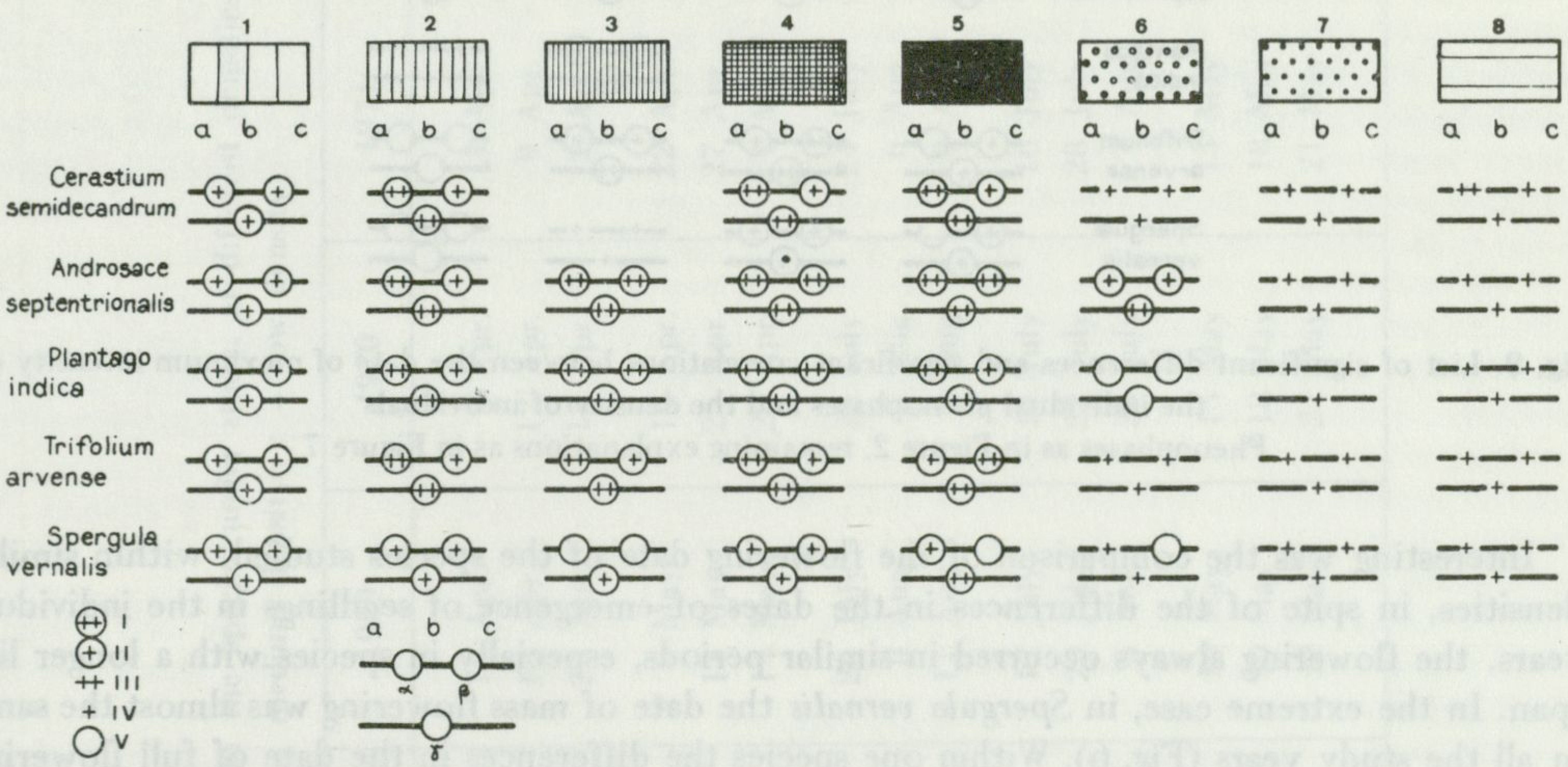

Fig. 7. List of significant differences and correlation between the duration of individual phenophases and the density of individuals

Phenophases as in Figure 2. α – relationship between high density and medium density, β – relationship between medium density and low density, γ – relationship between high density and low density. I – significant differences and significant negative correlation each year, II – significant differences and significant negative correlation in some years, III – significant differences each year, but no correlation, IV – significant differences in some years, but no correlation, V – non-significant differences

remaining species, and for all the species in the remaining developmental stages density has not been found to affect the duration of the following phases: of unripe fruits, ripe fruits and dissemination, and of dying. It must be emphasized, however, that under the conditions of a heavy overcrowding, a mass dying of individuals reduces the differences between the "high", "medium" and "low" densities in the fruiting phase, as compared with the seedling phase (cf. the survivorship curves, Figs. 2–6). It is, therefore, possible that this was the reason why no linear relationship was found between the density and the duration of the terminal life phases (Fig. 7). In spite of this, in as many as three species the date of maximum dying, and in four species the date of the maximum intensity of ripe fruit and dissemination differed significantly in individuals growing at different densities (Fig. 8). Obviously, these differences were yet greater in the case of the earlier developmental phases: of flower buds and of flowering. In *Trifolium arvense* and *Plantago indica*, for instance, the maximum intensity of the flowering phase of the individuals at a hight density always occurred 14–21 days earlier than at a low density, while the greatest, in the study period, differences in the date of maximum fruiting and dissemination of these species amounted to 12 days. Thus the acceleration of development at a high density is particularly evident until the flowering time (cf. P a l m b l a d 1968).

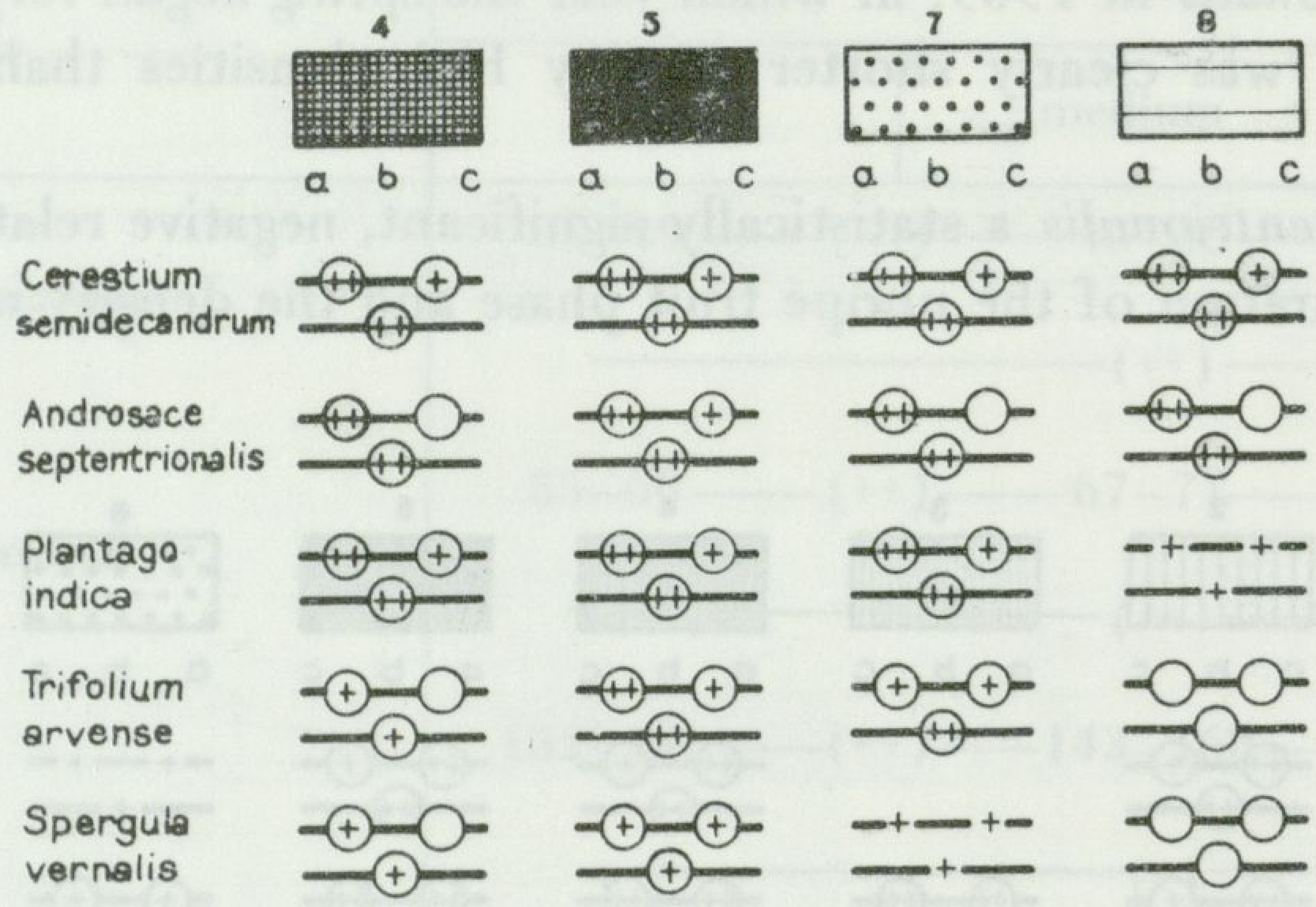

Fig. 8. List of significant differences and significant correlations between the date of meximum intensity of the individual phenophases and the density of individuals
Phenophases as in Figure 2, remaining explanations as in Figure 7

Interesting was the comparison of the flowering date of the species studied: within similar densities, in spite of the differences in the dates of emergence of seedlings in the individual years, the flowering always occurred in similar periods, especially in species with a longer life span. In the extreme case, in *Spergula vernalis* the date of mass flowering was almost the same in all the study years (Fig. 6). Within one species the differences in the date of full flowering were found to be in general greater in the same year at different densities than at similar densities but in different years (Table II). Only in 1969 was a significantly delayed, relative to the remaining years, flowering observed in *Cerastium semidecandrum*, and especially in *Androsace septentrionalis;* but even in this case statistically significant differences were found in the date of flowering between individuals occurring at different densities. It may, therefore, be concluded that a biotic factor such as the population density, can to a larger extent modify the development of individuals, determined primarily by the biological characteristics of the species, than can a complex of climate or habitat conditions.

4. CONCLUSIONS

The studies permit the following conclusions to be put forward:

1. The length of life of the individuals of the annual species studied depends both on the climatic conditions and the density of a population. The climatic conditions determine the germinating date and the duration of the seedling phase, a retarded growing always causing an acceleration of the occurrence of the successive phenophases and shortening of the life history. The stimulating effect of a high density on the rate of development is most marked in the period preceding the date of flowering.

2. The studies have in essence confirmed the view held by S u k a č e v (1941) that under adverse conditions affecting the growth of the annuals due to population overcrowding, there

Table II. Dates of full flowering of the species under study, at different densities
a — high density, b — medium density, c — low density

Species	Density	1968	1969	1970	1971	1972	1973
Cerastium semidecandrum	a	4 Apr.	11 Apr.	6 Apr.	3 Apr.	4 Apr.	3 Apr.
	b	10 Apr.	17 Apr.	12 Apr.	9 Apr.	10 Apr.	9 Apr.
	c	13 Apr.	23 Apr.	15 Apr.	12 Apr.	14 Apr.	12 Apr.
Androsace septentrionalis	a	20 Apr.	8 May	19 Apr.	22 Apr.	21 Apr.	21 Apr.
	b	26 Apr.	11 May	25 Apr.	27 Apr.	28 Apr.	29 Apr.
	c	29 Apr.	14 May	28 Apr.	1 May	30 Apr.	30 Apr.
Plantago indica	a	25 July	26 July	23 July	24 July	23 July	22 July
	b	6 Aug.	8 Aug.	5 Aug.	6 Aug.	7 Aug.	4 Aug.
	c	10 Aug.	11 Aug.	8 Aug.	9 Aug.	10 Aug.	8 Aug.
Trifolium arvense	a	15 July	17 July	14 July	16 July	17 July	13 July
	b	25 July	29 July	23 July	28 July	28 July	22 July
	c	28 July	5 Aug.	26 July	4 Aug.	4 Aug.	26 July
Spergula vernalis	a	14 May	16 May	15 May	14 May	16 May	15 May
	b	17 May	19 May	18 May	18 May	19 May	18 May
	c	20 May	22 May	21 May	21 May	22 May	21 May

occurs and acceleration of the phenological development. However, deviations from this rule have been found in the case of annual species with longer life cycles.

5. SUMMARY

During a six years' period the life cycles were observed of five species of annual plants at three different density levels. The investigations were carried out on dunes in the Toruń Basin in the years 1968–1973. A concise description of the weather conditions during the study period has been presented in Walter's climatic diagrams (W a l t e r 1962) – Figure 1.

The species under study differed in respect of the dates and the course of the successive phenophases and the total life length. Listed in order of ascending life spans they were: *Cerastium semidecandrum, Androsace septentrionalis, Plantago indica, Trifolium arvense* and *Spergula vernalis.* The developmental stage of the individuals was determined on the basis of 7–8 phenophases. In the comparative analysis of the developmental rhythmicity of the given species at different density levels the following were taken into account: (1) total length of the life cycle, (2) duration of the successive developmental phases,(3) date of attaining maximum intensity of the phase of flower buds, flowering, ripe fruits and seed dissemination and of dying – relative to the date of the first coming up of germs, and (4) the full flowering date.

In the verification of the statistical hypotheses the 0.05 level of significance was used.

The present studies permit a number of conclusions to be put forward:

1. The life span of the individuals of the species studied depends above all on the date of seedling emergence. A delay in the coming up process causes an acceleration of the successive phenophases and a shortening of the life cycle (Figs. 2–6, Table I).

2. An increase in the density of individuals of the annual species is followed by an acceleration of the phenological development. The shorter the life cycle of a species, determined by its biological properties, the more marked is this acceleration (Figs. 2–6).

3. The acceleration of development at a high density level affects in the first place the early developmental stages; in the post-flowering period density as a rule has no apparent effect on the duration of the individual phenophases (Fig. 7).

4. Due to their faster development, observed at high densities until the time of flowering, the individuals also attain at an earlier time their full fruiting and seed dissemination phases and they die earlier, relative to the individuals growing at lower densities (Fig. 8).

5. The seedling emergence date and the duration of the seedling phase, varying considerably from year to year, indicate that at the earliest developmental stage the climatic conditions play the most important role (cf. Fig. 1 and Figs. 2–6).

6. After the completion of the seedling phase a predominance of the effect of the inner rhythmicity of the species over the action of the broadly understood climatic factors could be seen in all the species studied. This is indicated by the similar dates of mass flowering in the different years, in spite of the differences in the dates of seedling emergence, and in the weather conditions of the individual years (Fig. 1, Table II).

Thus the studies have in essence confirmed the opinion put forward by S u k a č e v (1941) that in the annuals an overcrowding of individuals accelerates the development. However, this rule applies to species with very short life cycles.

6. POLISH SUMMARY

Przez okres sześciu lat obserwowano przebieg cyklów życiowych pięciu jednorocznych gatunków roślin w trzech różnych zagęszczeniach. Badania przeprowadzono na wydmach Kotliny Toruńskiej w latach 1968–1973. Syntetyczną charakterystykę warunków klimatycznych w okresie badań przedstawiono na diagramach klimatycznych Waltera (W a l t e r 1962) (rys. 1).

Uwzględnione w badaniach gatunki różniły się pod względem terminów i przebiegu kolejnych fenofaz oraz całkowitej długości życia. Wymienione w kierunku wzrastającej długości życia były to: *Cerastium semidecandrum, Androsace septentrionalis, Plantago indica, Trifolium arvense* i *Spergula vernalis.* Stan rozwojowy osobników oceniano na podstawie 7–8 fenofaz. W analizie porównawczej rytmiki rozwojowej badanych gatunków w różnych stanach zagęszczenia uwzględniono: 1) całkowitą długość cyklu życiowego,

2) czas trwania poszczególnych faz rozwojowych, 3) moment osiągania szczytu fazy pączków kwiatowych, kwitnienia, owoców dojrzałych i rozsiewania nasion oraz fazy usychania – w stosunku do daty pierwszych wschodów i 4) datę pełni kwitnienia.

W weryfikacji hipotez statystycznych zastosowano poziom istotności 0.05.

Przeprowadzone badania pozwalają na sformułowanie kilku wniosków:

1. Długość życia osobników badanych gatunków uzależniona jest przede wszystkim od terminu pojawiania się siewek. Opóźnienie wschodów powoduje przyśpieszenie kolejnych fenofaz i skrócenie cyklu życiowego (rys. 2–6, tab. I).

2. Wraz ze wzrostem zagęszczenia osobników jednorocznych gatunków roślin następuje przyśpieszenie rozwoju fenologicznego. Zaznacza się ono tym silniej im krótszy jest cykl życiowy danego gatunku, wynikający z jego właściwości biologicznych (rys. 2–6).

3. Przyśpieszenie rozwoju w warunkach dużego zagęszczenia dotyczy przede wszystkim wczesnych faz rozwojowych; po przekwitaniu na ogół nie zaznacza się już wpływ zagęszczenia na długość poszczególnych fenofaz (rys. 7).

4. Szybszy rozwój osobników w dużym zagęszczeniu do momentu kwitnienia powoduje, że wcześniej osiągają one także pełnię owocowania i rozsiewania nasion i wcześniej zamierają, w porównaniu z osobnikami wyrosłymi w małym zagęszczeniu (rys. 8).

5. Termin wyrastania siewek oraz długość fazy siewki, wykazująca duże wahania z roku na rok, wskazują na to, że w najwcześniejszym etapie rozwoju decydujący wpływ wywierają czynniki klimatyczne (por. rys. 1 oraz rys. 2–6).

6. Po przejściu fazy siewki zaznacza się u wszystkich badanych gatunków przewaga wpływu wewnętrznej rytmiki gatunku nad działaniem szeroko pojętych czynników klimatycznych. Świadczy o tym zbliżona w różnych latach data masowego kwitnienia, mimo różnic w terminach wyrastania siewek i w warunkach pogodowych poszczególnych lat (rys. 1, tab. II).

Badania potwierdziły zatem w zasadzie opinię Sukačeva (1941), że u jednorocznych gatunków roślin przegęszczenie powoduje przyśpieszenie rozwoju. Zasada ta dotyczy jednak gatunków o bardzo krótkim cyklu życiowym.

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