

EKOLOGIA POLSKA (Ekol. pol.)	31	4	839-881	1983
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POPULATION SIZE REGULATION AS A RESULT  
OF INTRA-POPULATION INTERACTIONS

I. EFFECT OF DENSITY ON THE SURVIVAL AND DEVELOPMENT  
OF INDIVIDUALS OF EROPHILA VERNA (L.) C. A. M.

ABSTRACT: Population dynamics of the annual Erophila verna in the Festuco-Koelerietum glaucae Klika 1931 was studied for seven years. It has been demonstrated that an increased density in a seedling population brings about a significant intensification of interactions between individuals. As a result, the death rate rises, the life history is shortened, and the fraction of generative individuals becomes reduced. The survival of a population may follow type I, II or III of Deevy's (1947) curve, depending on the density. A close relationship has been found between the course of seasonal variation in numbers and the spatial structure of a population.

KEY WORDS: Sand dunes, Erophila verna, survival curves, seasonal abundance dynamics, density-dependent mortality, phenological development of individuals, life history of the population of an annual.

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## 1. INTRODUCTION

Environmental, and especially abiotic, conditions reduce the hereditary chance of individuals to survive and produce offspring, regardless of whether they are free of pressure from other members of the population or are subject to it throughout their life. Biotope and biocoenotic factors have therefore been commonly ascribed a key role in the limitation of population abundance (Chadwick and Dalke 1965, Harper, Williams and Sagar 1965, Baskin and Baskin 1979, Barkham 1980, Bentley, Whittaker and Malloch 1980, Gilbert 1980, Gross 1980, Inoué, Beyers and Brown 1980). At the same time, the results of many studies indicate that the influence of the environment can be significantly modified by various forms of intra-population interactions, as a result of which the limiting effect of weather, soil and phytocoenotic factors on the abundance of a plant population is weakened or intensified (Palmblad 1968, Noble, Bell and Harper 1979, Symonides 1979a, 1979b, 1979c, Law 1981).

Studies of the interactions between individuals of the same plant species under natural conditions, and particularly an evaluation of their real role in the regulation of population size are

connected with many methodical difficulties. There are several causes of this. Firstly, a situation in which a population functions in a "competitive vacuum" is an exception. Members of a population as a rule neighbour other phytocoenose components, which makes it difficult, or even impossible to precisely separate the effects of intraspecific competition from those caused by interspecific competition (Harper and Chancellor 1959, Harper and McNaughton 1962, Zarzycki 1965, Rabotnov 1969). Secondly, interactions between plants of the same species or of different species are accomplished almost exclusively via the environment: by way of transforming the biotope and biocoenotic relations (Andrzejewski and Symonides 1982). Thus the quality of the environment may determine both the kind and intensity of the interactions between individuals. A natural consequence of this relationship may be different effects of interactions in different places of the entire population area. Thirdly, the environment-transforming potential of organisms and their sensitivity and reactions to the transformations depend on their age, developmental phase, size and condition (Symonides 1979a, 1979b, Law 1981). This causes a complex system of intra-population relations to arise, especially in the case of a varying density in the area of a biotope, a varied age structure of the population and a mosaic-like biotope. At the present stage of knowledge it is thus possible only to indicate certain components of intra-population interactions affecting the abundance dynamics, and only in a generalized, qualitative way.

In the present series of studies a trial was undertaken for quantifying the effect of the interactions between individuals on seasonal and many-years' changes in numbers of a natural plant population. It was not by chance that the studies comprised a population of Erophila verna, a small annual, the whole life history of which is completed in early spring, and which inhabits relatively homogeneous, infertile, scantily overgrown sand areas. The choice of the study object was dictated by the necessity to eliminate the interactions between individuals of different age, and to obtain the highest possible limitation of the effect of interspecific competition and spatial diversity of the biotope on the intra-population relations.

As it is known, changes in numbers of populations of organisms permanently attached to the substrate are the resultant of fecundity and mortality. On account of the aim of the study, the course of the two processes was observed for several years under the conditions of a varied intensity of intra-population interactions, i.e., within natural, spatially delimited aggregations consisting of a varying number of individuals, with a varying distance separating them. The starting point of these studies was four basic assumptions: (1) the intensity of interactions between even-aged individuals is the function of, primarily, the distances that separate them, (2) with equal distances, the efficiency of interactions depends on the developmental phase and the size of the individuals, (3) the range of the interactions of sedentary organisms is practically restricted to the immediate vicinity, and (4) the kind and intensity of intra-population interactions may vary from year to year as a result of different weather conditions during the growth and development of individuals.

To supplement the field investigations, a number of experiments has been carried out aimed at, among other things, determining the viability of seeds and their ability to germinate, and the survivorship and differentiation of individuals in laboratory systems, under equalized abiotic conditions with a variable, as in the natural population, density.

The results of the studies will be presented in three separate papers. The aim of the first (this) paper is an analysis of the seasonal variations in population abundance and of the effect of the interactions between individuals on their survival and development. The next paper (Symonides 1983) will contain the results of investigations into the morphological differences between individuals that grew under different density conditions, and their role in the control of population size. The experimental part will be presented in the third paper (Symonides - in press) which also will contain summing-up conclusions on intra-population abundance-limiting and abundance-regulating mechanisms in an E. verna population.

## 2. METHODS

Field studies were carried out in the years 1968-1974 in a floristically poor patch of Festuco-Koelerietum glaucae found at

the edge of a sand dune in the Toruń-Basin<sup>1</sup>. Apart from the species whose names appear in the name of the association, and which make up the community, it was possible to encounter, here and there, single individuals of dicotyledon perennials (Table I). Only in early spring were gaps between grass tussocks bridged by small E. verna plants with white flowers.

Table I. Floristic composition of the vegetation in the study areas

Species	Flowering period
<u>Erophila verna</u> (L.) C. A. M.	April-May
<u>Festuca psammophila</u> (Hackel) Krajina	June-July
<u>F. duriuscula</u> L.	June-July
<u>Koeleria glauca</u> (Schkuhr) DC.	June-July
<u>Gypsophila fastigiata</u> L.	June-August
<u>Jasione montana</u> L.	July-September
<u>Centaurea rhenana</u> Bor.	July-September
<u>Artemisia campestris</u> L.	July-September
<u>Hypericum perforatum</u> L.	July-August
<u>Thymus serpyllum</u> L.	July-September

Observations of the survival and development of E. verna individuals were carried out in four permanent areas each of the size of 4 m<sup>2</sup>, divided into 0.01 m<sup>2</sup> plots. Each day during the seed germinating season, and every three days in the remaining phases individuals found in the plots were counted, and the state of their development was assessed. The data obtained were subsequently used for working-out the spatial structure and abundance dynamics over seasonal and many-years' cycles, and for determining the number of survivors at the end of the growing season of the population, and the number of individuals attaining generative phases in the particular years.

The effect of the interactions between individuals on their survival and development was analysed on the basis of data from plots appropriately selected for the number of seedlings and dis-

<sup>1</sup>A detailed description of the soils, climate and vegetation of the study area can be found in the paper of Symonides (1974).

tances between them. Five plot classes (representing five density classes) were chosen with the following numbers of seedlings: class I - 1-2, class II - 5-10, class III - 15-30, class IV - 35-50, class V - 55 or more. The distances between seedlings in the plots of the above classes were as follows: 10-12 cm, 2-4 cm, 1.0-1.5 cm, 0.4-0.8 cm and below 0.2 cm, respectively. Though the number of plots in the different years varied, there always occurred in them 70.3% (in 1970) to 84.6% (in 1973) of the total number of individuals growing in the study areas.

To obtain a complete picture of the relationship between seedling density and population survival, the average percentage was calculated of individuals per each  $0.01 \text{ m}^2$  at the successive observation dates. The number of seedlings recorded in those plots which were analysed jointly on account of their representing a similar density class was adopted as 100%. On this basis curves have been drawn of seasonal variations in abundance for a varying intensity of intra-population interactions. Average longevity has also been assessed for the density classes distinguished, as well as average percentage of individuals completing their life history (fruiting). For both characters an interval estimation has been made and the correlation coefficient has been calculated, assuming the level of error risk of 0.05 (Okta 1977).

In the further elaboration of the results curves have been plotted of E. verna survival in different density classes on the basis of average values for seven growing seasons. Regardless of its length, the life history of the population was treated as unity, whereas the survivorship of individuals was determined in intervals of  $1/24$  of the life history. The aim of this procedure was to find whether there is a clear relationship between the survivorship curve type and population density in spite of the varying weather conditions and duration of the life history.

The course of the phenological development of individuals under different density conditions has been presented in spectra prepared by Beideman's (1954) method. The following phenophases have been marked in them: (1) seedling, (2) vegetative growth, (3) budding, (4) flowering, (5) fruiting, (6) dissemination, (7) dying of plants. The spectrum scale is always comparable, because assumed as 100% for each date of observation is the total number of individuals found in plots analysed jointly, on account of a similar density. Vertically, the number of phases

Table II. Description of the weather conditions during the life history of *E. verna*.

Year	Date of disappearance of snow cover	Month	Ten-day period	Average air temperature (°C)	Total precipitation (mm)	Number of days with an air temperature of			Number of days with ground frost	Number of days with rainfall
						< 0°C	> 5°C	> 10°		
1	2	3	4	5	6	7	8	9	10	11
1968	19th March	March	I	-1.2	6.7	7	-	-	8	3
			II	0.5	10.9	4	-	-	5	8
			III	9.6	5.7	-	10	5	-	2
		April	I	6.3	11.7	-	6	2	2	5
			II	6.1	1.6	-	5	2	7	2
			III	14.9	16.9	-	10	10	-	5
		May	I	13.0	6.0	-	9	8	-	5
			II	9.9	34.7	-	9	5	1	8
		1969	31st March	March	I	-3.7	1.6	10	-	-
II	-2.6				5.5	10	-	-	10	3
III	0.5				7.9	2	-	-	9	5
April	I			4.1	1.5	-	4	-	7	3
	II			4.7	31.9	1	5	-	4	8
	III			8.0	5.9	-	8	3	2	4
May	I			15.5	19.4	-	10	9	-	6
	II			15.4	10.2	-	10	10	-	4
1970	2nd April			March	I	-1.6	27.0	8	-	-
		II	-0.5		11.3	5	-	-	7	6
		III	1.1		11.9	3	1	-	9	7
		April	I	2.8	44.2	1	3	-	3	7
			II	5.8	25.9	-	5	2	3	7
			III	8.5	28.1	-	9	3	1	8
		May	I	11.9	41.1	-	8	6	2	3
			II	11.9	64.9	-	10	8	-	4

Table II (continued)

1	2	3	4	5	6	7	8	9	10	11
1971	16th March	March	I	-6.2	3.3	8	1	-	10	6
			II	3.2	9.3	2	2	-	5	5
			III	4.3	6.0	1	4	1	2	4
		April	I	9.3	11.2	-	10	3	-	4
			II	6.7	3.2	-	7	1	4	1
			III	4.9	24.5	-	5	2	3	7
		May	I	9.7	-	-	9	5	2	-
			II	18.9	7.5	-	10	10	-	2
		1972	12th March	March	I	2.0	8.9	-	-	-
II	2.4				-	2	5	-	9	-
III	5.4				21.1	-	6	-	3	7
April	I			7.8	14.4	-	8	1	1	4
	II			7.9	10.2	-	10	2	-	3
	III			6.4	5.6	-	7	1	5	4
May	I			12.2	3.9	-	10	9	-	3
	II			12.0	58.1	-	10	7	-	9
1973	2nd March			March	I	2.2	4.6	1	1	-
		II	1.6		21.6	2	-	-	8	7
		III	8.3		-	-	11	3	1	-
		April	I	4.7	21.0	-	5	-	4	8
			II	3.6	11.9	-	2	-	7	7
			III	8.8	1.0	-	3	3	1	1
		May	I	12.5	27.7	-	10	7	-	8
			II	9.7	9.7	-	10	4	2	7
		1974	4th March	March	I	1.0	-	1	-	-
II	4.9				7.4	-	4	-	4	3
III	6.9				-	-	7	1	6	-
April	I			8.0	-	-	10	-	2	-
	II			5.2	-	-	4	1	6	-
	III			7.2	8.1	-	9	2	3	8
May	I			8.9	25.6	-	10	5	-	5
	II			12.5	0.3	-	10	9	-	1



recorded on an observation day can be read, and marked horizontally is their duration. Similar spectra have been worked out for the whole population in the successive study years.

The statistical analysis of the data from phenological observations takes into account the duration of the vegetative and generative phases of individuals found in the plots of the different classes, separately for each year. The zero hypothesis of a lack of significant differences between densities in respect of the characters studied has been verified by the analysis of variance in single classification, assuming the 0.05 level of error risk (G r e ń 1974).

The relationship between the density of seedlings and their mortality, density of seedlings and the mortality of individuals before the full development of the population (full fruiting period), and the density of seedlings and the fraction of individuals that attained the generative phase was estimated on the basis of the coefficients of correlation and of regression calculated from the mean values for seven years. In this case taken into account were only data from plots differing exactly by 5 seedlings in the interval of 1 to 56 seedlings. Confidence intervals for the regression coefficients have been assessed at the significance level of 0.05 (G r e ń 1974).

The course of the weather phenomena accompanying the seasonal development of E. verna populations in the successive ten-day periods of each month have been described by setting out the following parameters in tables: (1) average air temperature, (2) number of days with an average daily air temperature below 0°C, (3) number of days with an average daily air temperature above 5°C, (4) number of days with an average daily air temperature above 10°C, (5) number of days with ground frost, (6) total precipitation and (7) number of days with rainfall. The summary contains data from the Institute of Meteorology and Water Economy, Toruń-Wrzosy. From the author's own observations the data has been given of the complete disappearance of the snow cover in the study area (Table II).

### 3. RESULTS

#### 3.1. Population size and its spatial structure

During five consecutive years, from 1968 to 1972, the abundance of the population in the period of its seasonal peak differed

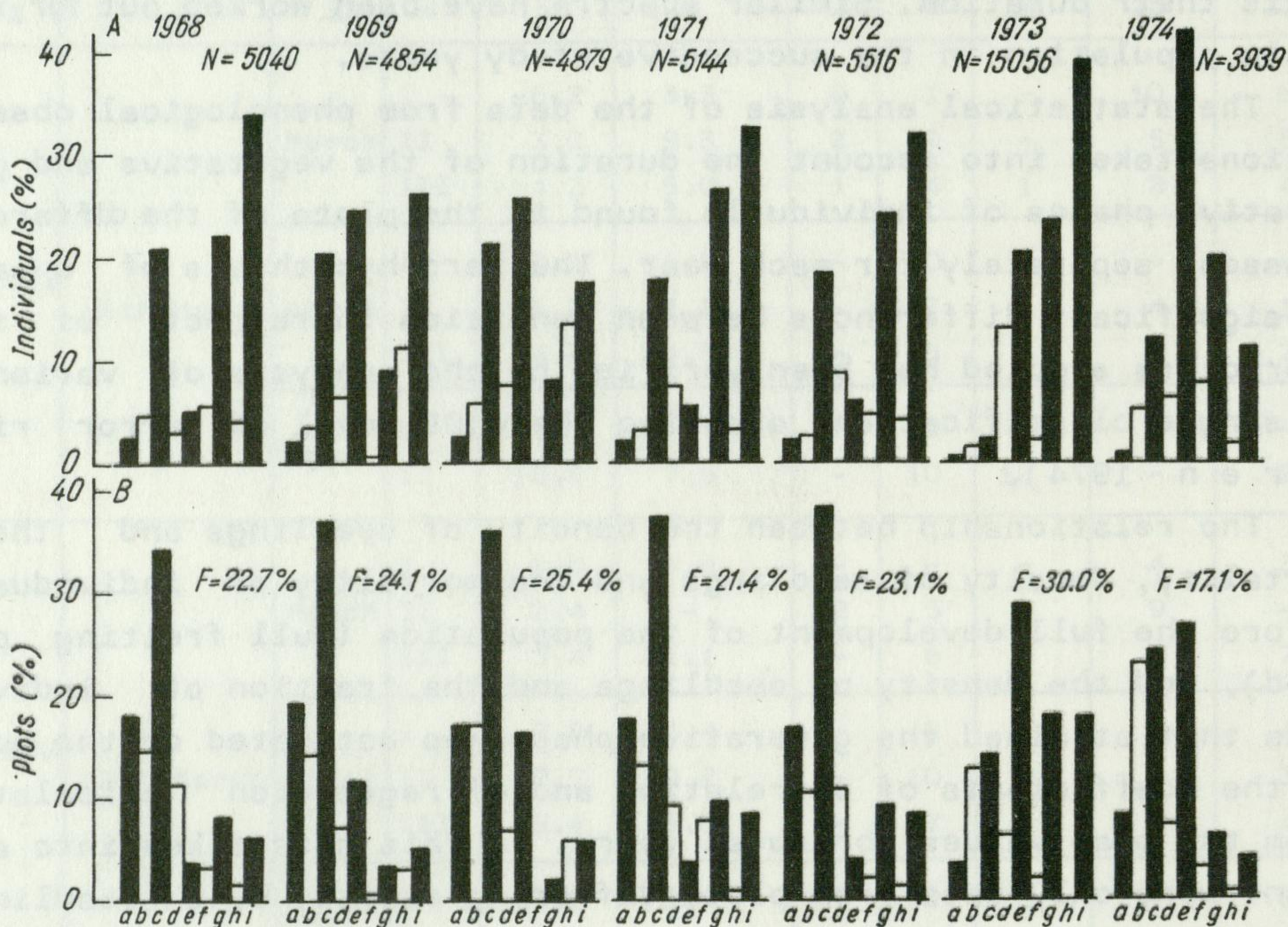


Fig. 1. Description of the spatial structure of *E. verna* population

A - percentage of seedlings in plots of the particular density classes, B - proportion of plots with a different number of seedlings: a - 1-2, b - 3-4, c - 5-10, d - 11-14, e - 15-30, f - 31-34, g - 35-50, h - 51-54, i -  $\geq 55$ , N - total number of seedlings emerged in study areas, F - frequency of the population at seasonal peak numbers. Dark columns - individuals and plots taken into account in the detailed analysis of survival and development of *E. verna*

slightly. Small too was the degree of variation, from year to year, in population density and in the proportions of the plots representing density classes (Fig. 1). In 1973, there was a significant increase in numbers of the population, over three-fold, relative to the average for the period considered. In that year also the highest values were recorded of frequency, average population density per  $1 \text{ m}^2$ , maximum density in plots (up to 127 seedlings per  $0.01 \text{ m}^2$  area), and the highest fraction of class V plots. In the following growing season, in 1974, already, all these parameters took the lowest values for the seven-year study period.

Fluctuations in numbers and frequency did not affect the spatial structure type of the population. Throughout the study pe-

riod the structure remained highly aggregative. This is indicated first of all by a low frequency with an immense number of seedlings growing every year. In 1126-1326 out of the 1600 plots in the study areas not even one E. verna individual was found. The frequency did not change during the growing season (in 1968, 1970 and 1973) or dropped insignificantly: by from 0.2% (in 1969) to 1.0% (in 1974).

An aggregative population spatial structure type in the period of the seasonal peak is further indicated by a relatively high, although different in different years, proportion of plots with a large number of seedlings. Highly aggregated clumps, each consisting of at least 51 seedlings, contained jointly from 30.4% (in 1970) to 38.5% (in 1973) of the total number of young individuals; only in 1974 were considerably fewer, only 14.4%, seedlings found in such plots (Fig. 1).

Noteworthy was the course of abundance dynamics of the seedlings in the individual plots in the successive study years. Plots with a small number of individuals in the first study year represented high density classes in the next growing season, and then only a few seedlings grew on them. In places where very dense aggregations were found in 1968 several seedlings at the most were found the following year, whereas two years later the density in these plots was again very high (Fig. 2). These great variations in numbers in plots with very low and very high densities recurred consistently throughout the study period, and involved nearly all the plots chosen for the detailed analysis of the survival and development of the individuals found in them. In some cases, however, few seedlings were found in the same plots in 2-3 consecutive years, but never was an identical location of very dense aggregations recorded.

In addition, a remarkable feature of the spatial structure of an E. verna population is a dispersed occurrence of individuals or their aggregations within the biochore. Thus there are no clear zones of "aggregation" and of "thinning"; with a few exceptions single individuals or groups inhabited plots clearly separated spatially from one another. They were usually the same plots in consecutive years; only in 1973, when the population grew in numbers relative to the previous years, did seedlings appear also in many formerly unoccupied plots (Fig. 2).

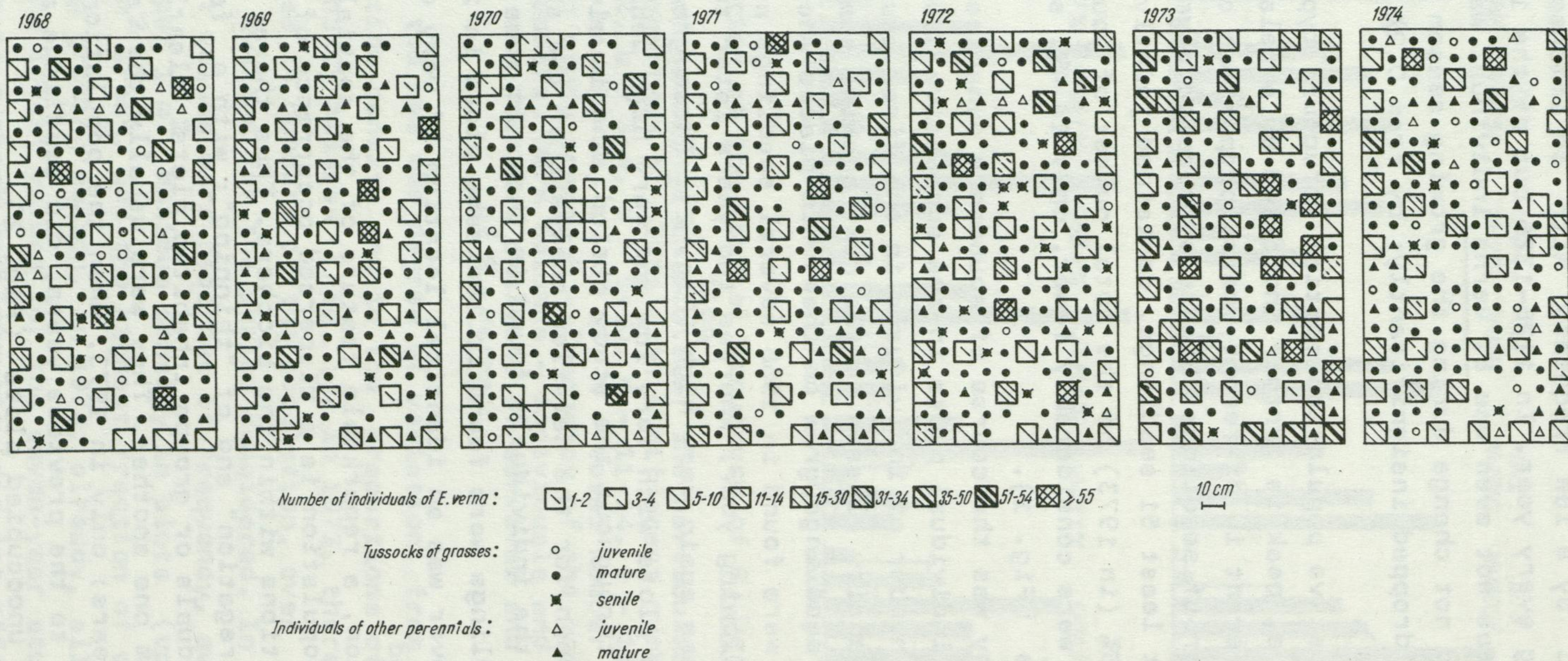


Fig. 2. Dynamics of the spatial structure of *E. verna* population in the study period  
The cartogram shows part of one of four study areas

### 3.2 Seasonal variations in population size

Each year the population dynamics shows fast changes in numbers during the growing season, these changes being particularly rapid during the period of seed germination (Fig. 3).

The time of appearance of the first seedling, and thereby of the seasonal beginning of a population is determined primarily by the date of disappearance of the snow cover and thawing of the surface soil layer (Table II). Thus the life history of the population began each year at a different date, from the first days of March (1973 and 1974), through the beginning of the calendar spring (1968, 1971 and 1972) until the first ten-day period in April (1969 and 1970).

Peak numbers are attained within only 2-7 days; this always occurs earlier if germination has been delayed; in 1970 as many as 90% of the total number of seedlings appeared within only 12 hours. From Figure 3 follows that the rate of attaining the seasonal peak does not depend on the number of seedlings appearing in the particular years. In 1973 and 1974, the course of development of the population was very similar, although the total number of germinated seeds differed considerably.

Regardless of the date of the first germs and the duration of the life history, the course of the dying of individuals at an early stage of the development of a population is similar. Each year the abundance curve drops immediately after attaining the peak: 10 days after the germination of the last seed 37.5% to 52.4% of individuals die, mainly in the seedling phase. The course of further elimination is in general much slower, although its intensity varies from year to year.

Only in 1968 was a complete stabilization of numbers found, falling on the middle of the life history of the population: for 9 days not a single individual died. In the years 1970-1972 also there was a slight decrease in numbers in the middle of the life history. In the other years the plants died gradually, independently of their age and phase of phenological development. Though the date of the beginning of germination varied considerably, the last individual of the population died at a very similar date each year: between May 16 and 22 (Fig. 3).

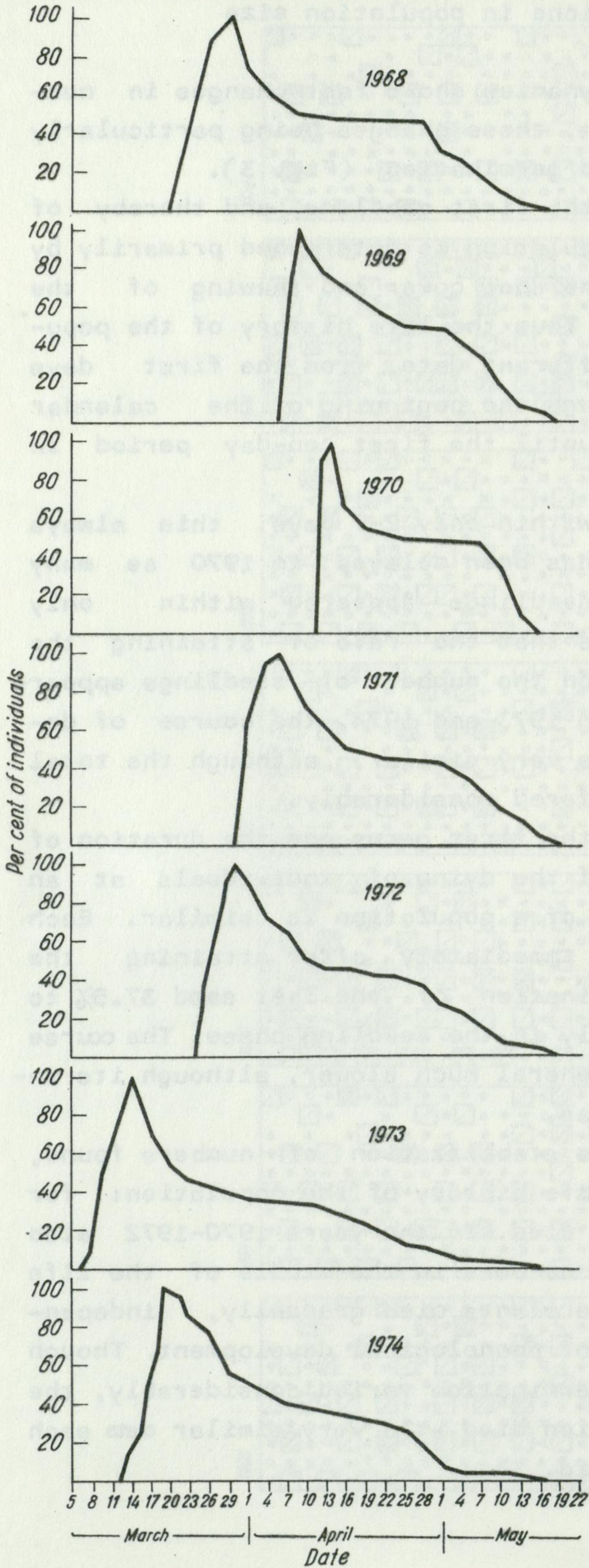


Fig. 3. Seasonal variations in numbers in E. verna population

100% - total numbers of seedlings emerged in the study areas

## 3.3. The course of population life history

The duration of the life history of the population varies considerably from year to year, and so does the date and duration of the particular phenophases (Fig. 4).

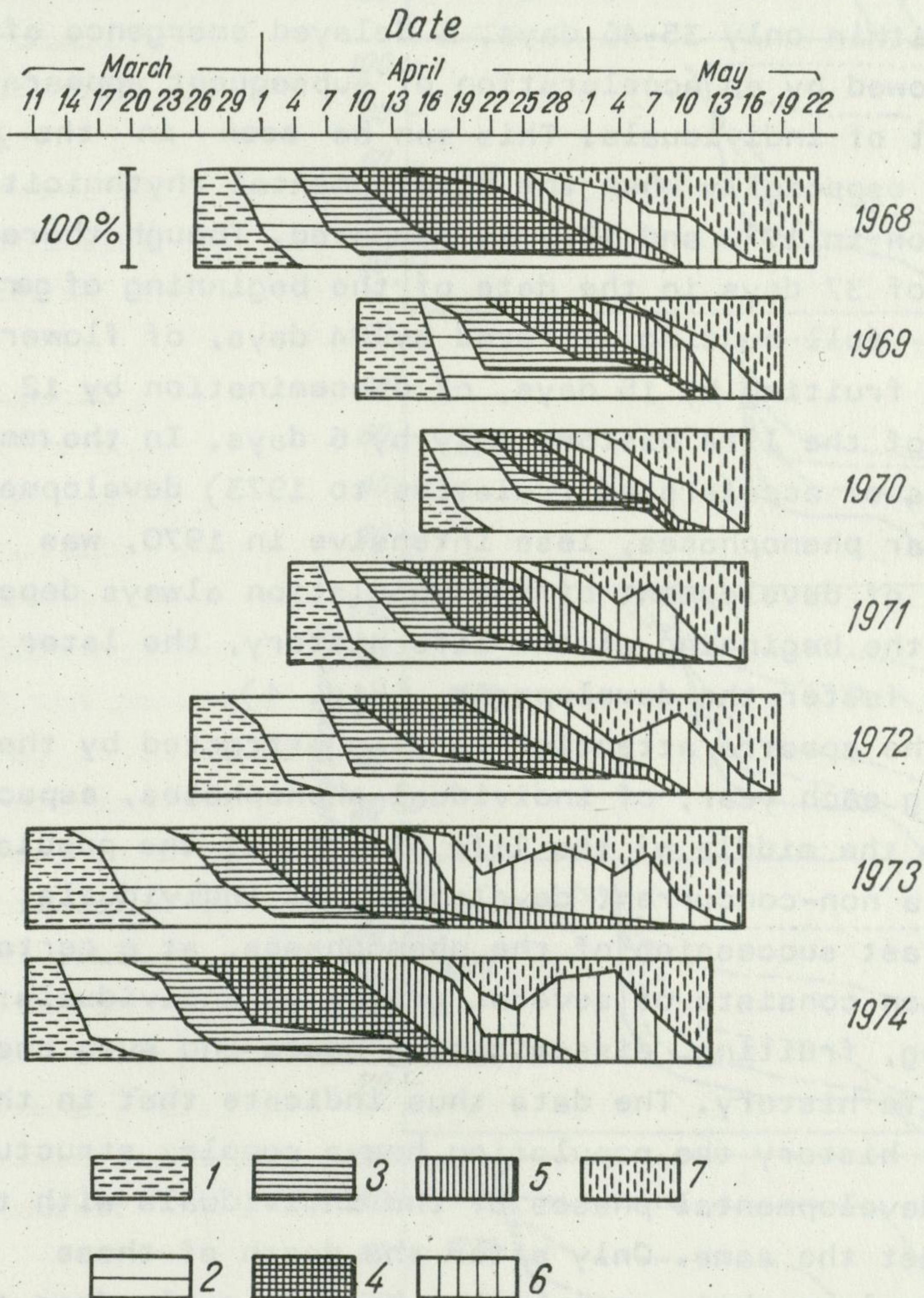


Fig. 4. Phenological spectra of E. verna population

100% - total number of individuals in the study areas at successive observation dates. Phenophases: 1 - seedling, 2 - vegetative growth, 3 - budding, 4 - flowering, 5 - fruiting, 6 - seed dissemination, 7 - dying of plants

The earliest seed germination was recorded in 1973 when the first seeds germinated as early as March 7, thus determining an early beginning of the life history of the population. The latest, relatively - on April 13 only - appearance of the first seedlings was recorded in 1970.

As the dates of the dying of individuals are similar, the duration of the life history is closely related with the date of seed germination. While with an early appearance of seedlings (in 1973 and 1974) the life history of the population lasts 66-71 days, in the case of a much delayed germination (1970 and 1969) it is completed within only 35-46 days. A delayed emergence of seedlings was followed by an acceleration of subsequent appearances and development of individuals. This can be seen in the phenological spectra, especially when the developmental rhythmicity of the population in 1970 and 1973 is compared. Though there was a difference of 37 days in the date of the beginning of germination, the dates of full budding differed by 24 days, of flowering by 18 days, of fruiting by 15 days, of dissemination by 12 days, and of the end of the life history only by 6 days. In the remaining years a process of accelerated (relative to 1973) development in the particular phenophases, less intensive in 1970, was found, but the rate of development of the population always depended on the date of the beginning of the life history, the later the beginning, the faster the development (Fig. 4).

In the spectra attention is also attracted by the overlapping, recurring each year, of individual phenophases, especially conspicuous in the middle of the life history of the population. It indicates a non-concurrent development of individuals, so in spite of the fast succession of the phenophases, at a certain time the population consists of several groups of individuals: juvenile, flowering, fruiting, disseminating seeds and even ones completing their life history. The data thus indicate that in the middle of the life history the population has a complex structure in respect of the developmental phases of the individuals with their age being almost the same. Only after the death of those individuals which complete their ontogenetic history early does the population return to a less complex structure; then it usually consists of two groups of plants: individuals disseminating seeds and those that are dying.

#### 3.4. Survivorship of individuals under different density conditions

The varying course of the curves illustrating the survival of individuals in plots analysed jointly for the number of seedlings



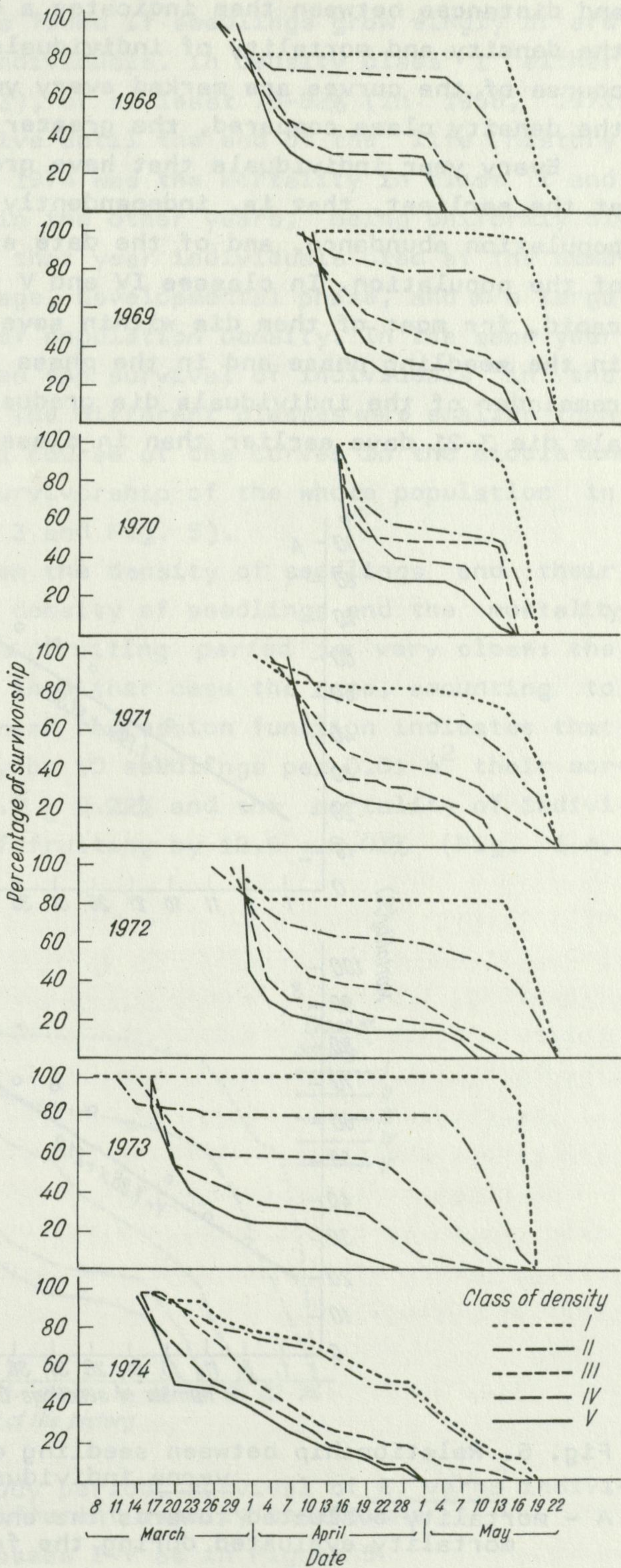


Fig. 5. Survival of *E. verna* individuals under different density conditions in successive study years

100% - total number of seedlings emerged in plots of the particular density classes: I - 1-2, II - 5-10, III - 15-30, IV - 35-50, V -  $\geq 55$

and distances between them indicates a clear relationship between the density and mortality of individuals. The differences in the course of the curves are marked every year, and the more different the density class compared, the greater the differences (Fig. 5).

Every year individuals that have grown at a high density die at the earliest, that is, independently of weather conditions, of population abundance, and of the date starting the life history of the population. In classes IV and V their elimination is fairly rapid, for most of them die within several to over a dozen days: in the seedling phase and in the phase of vegetative growth. The remainder of the individuals die gradually, yet the last individuals die 3-21 days earlier than in class I and II plots.

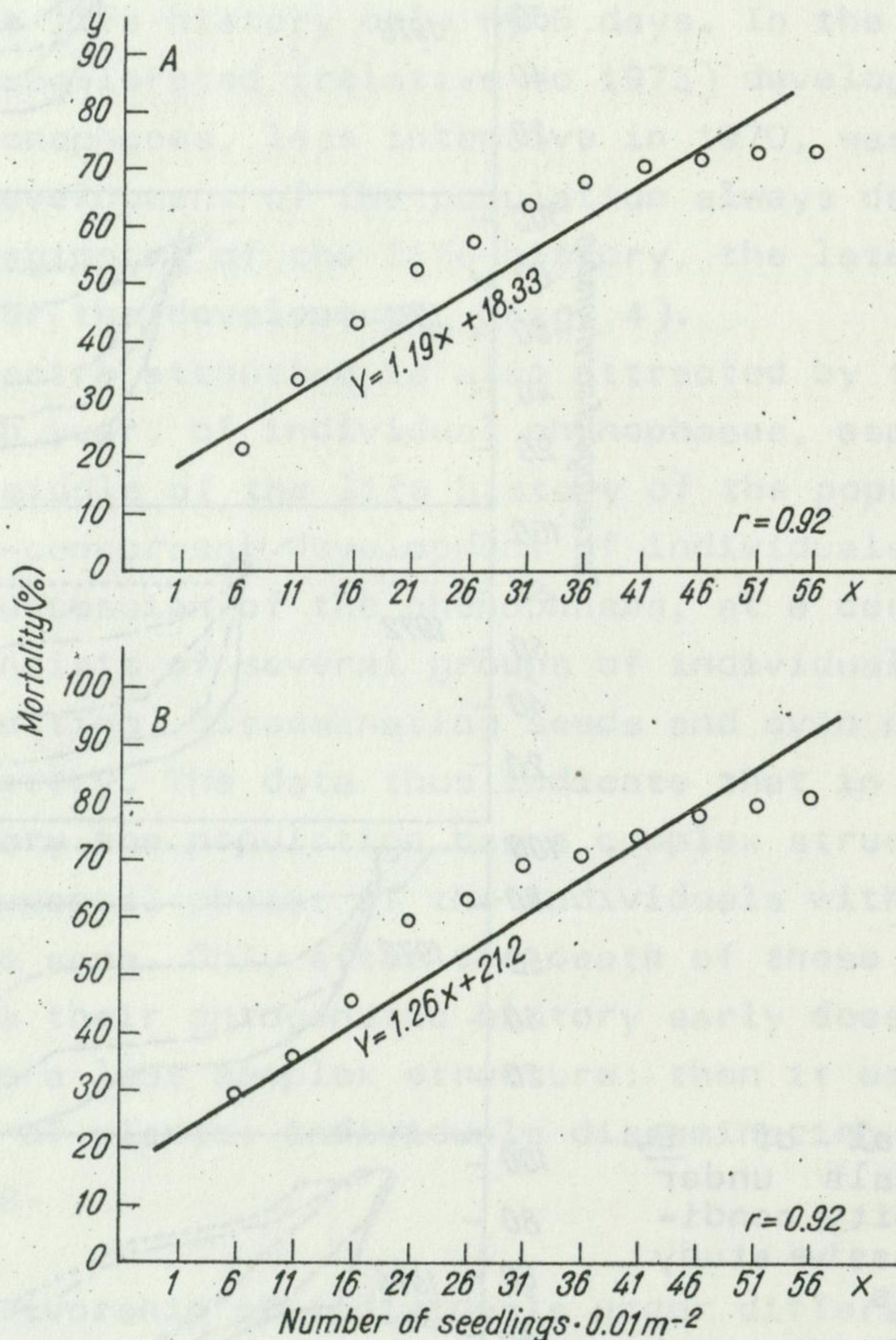


Fig. 6. Relationship between seedling density and mortality of *E. verna* individuals

A - mortality evaluated towards the end of the seedling phase, B - mortality evaluated during the fruiting of survivors

A converse situation is found if seedlings grow singly or are neighbored by few other individuals. In density class I either all (in 1969, 1970 and 1973), or at least 78-82% (in 1968, 1971 and 1972) of individuals live until the end of the life history of the population. Only in 1974 was the mortality in class I and II plots much higher than in the other years, being uniformly distributed against time. In that year individuals died at the same rate, regardless of their age, developmental phase, and to a large extent also independently of population density. In the same year also the differences between the survival of individuals in the growing season in plots of the different classes were smaller than in the remaining years. The course of the curves in the middle density class resembles the survivorship of the whole population in analogous years (cf. Fig. 3 and Fig. 5).

The relationship between the density of seedlings and their mortality, and between the density of seedlings and the mortality of individuals up till the fruiting period is very close: the correlation coefficient is in either case the same, amounting to 0.92. The course of the linear regression function indicates that with an increase in density by 10 seedlings per  $0.01 \text{ m}^2$  their mortality will increase by  $11.9 \pm 2.22\%$  and the mortality of individuals up till the period of fruiting by  $12.6 \pm 2.03\%$  (Fig. 6 A, 6 B).

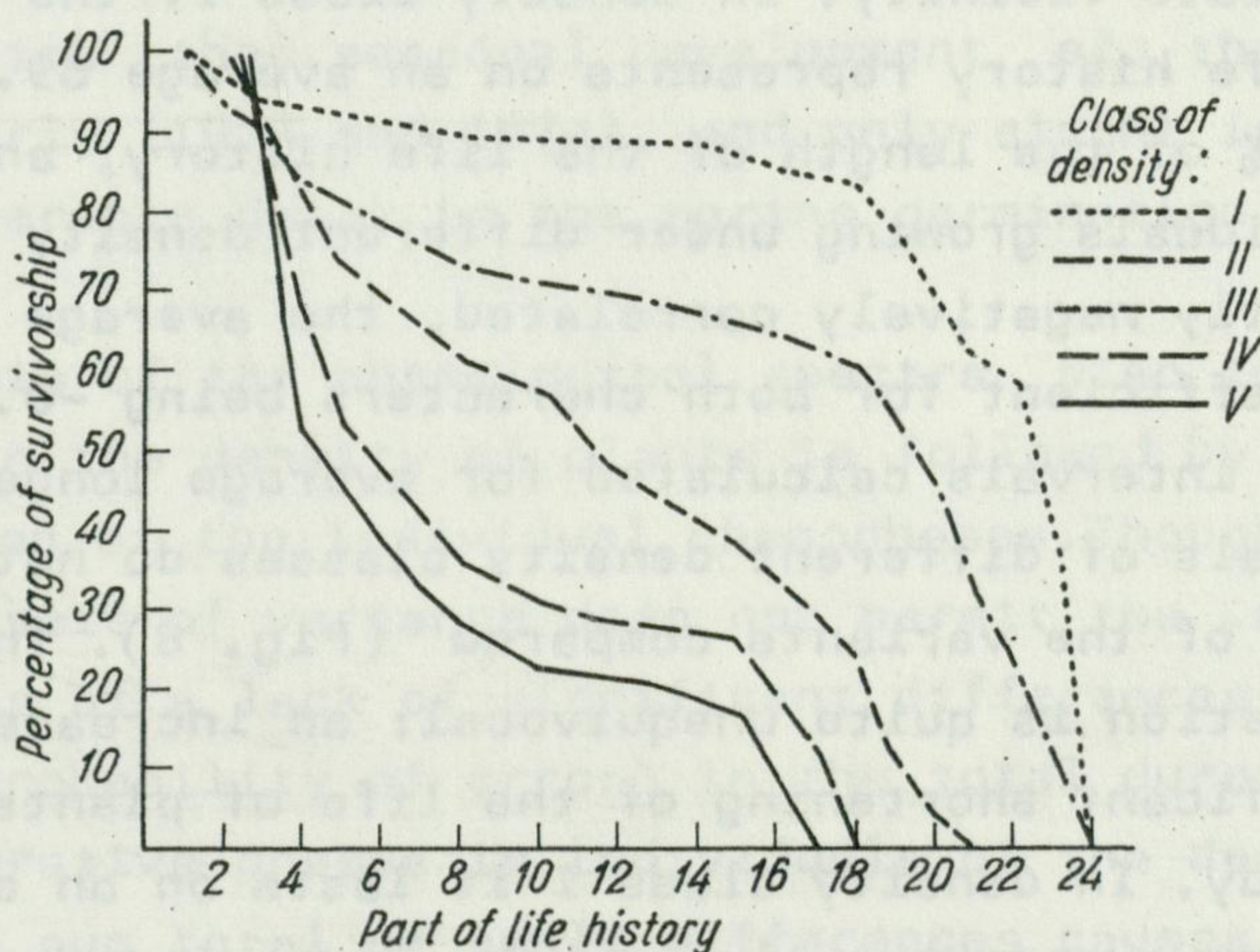


Fig. 7. Average, in the study period, survival of E. verna individuals under different density conditions

Density classes I-V as in Figure 5

Due to considerable differences in the duration of the life history of the population in the successive study years it is difficult to unequivocally interpret the course of the curves of survivorship in relation to density. For this reason, an average survival rate of individuals during seven years has been worked out in intervals equivalent to  $1/24$  of the life history of the population, regardless of its duration (Fig. 7). The results indicate that represented in a population - depending on the density of the different groups of individuals - are three classical survivorship types of Deevy (1947). Type one is found in the group of individuals of the lowest density class, type two - of the middle class, type three - of both the highest classes. Survivorship curves for class II plots show a great similarity to type two up to the middle of the life history, and to type one in its second part. The above elaboration also shows that in spite of their large numbers, representing  $45.6 \pm 15.8\%$  of the initial population, the proportion of individuals growing in plots of high density classes decreases quickly; in the middle of the life history of the population they constitute on the average only  $23.4 \pm 8.5\%$  of the total number of individuals.

The delayed seed germination in class IV and V plots, and above all the much earlier dying of individuals growing under high-density conditions indicate that individuals growing in aggregations live a shorter time than do those free from plant pressure in their immediate vicinity. In density class IV the total duration of the life history represents on an average 69.5%, and in class V - 63.4% of the length of the life history, and the longevity of individuals growing under different density conditions are significantly negatively correlated, the average value of the correlation coefficient for both characters being -0.69.

Confidence intervals calculated for average longevity of E. verna individuals of different density classes do not coincide or overlap in any of the variants compared (Fig. 8). The result of interval estimation is quite unequivocal: an increase in density causes a significant shortening of the life of plants of the species under study. In density class I it lasts on an average 23.2 days, and in the successive classes the longevity drops to 4.2, 1.4, 0.5 and 0.2 days, respectively. By comparison with individuals growing singly or far apart, the length of life of plants in heavily overcrowded aggregations is thus 116 times shorter. The

confidence interval values also indicate that in high density classes the longevity of individuals varies relatively little in the different years, but its variation is very great in the case of individuals inhabiting  $0.01 \text{ m}^2$  plots singly or in twos.

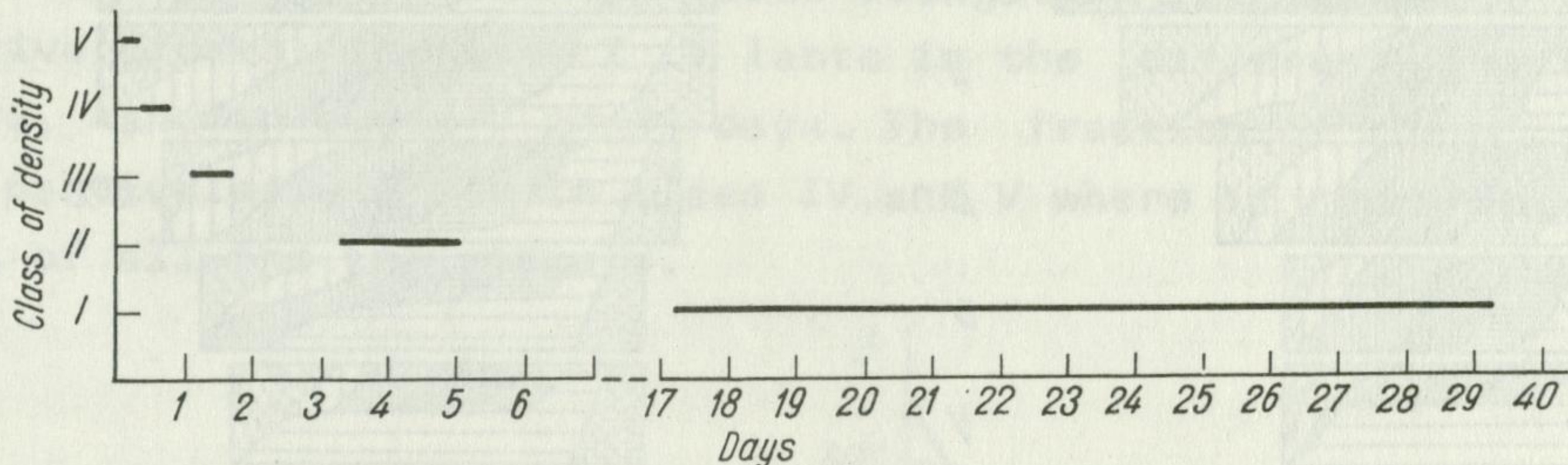


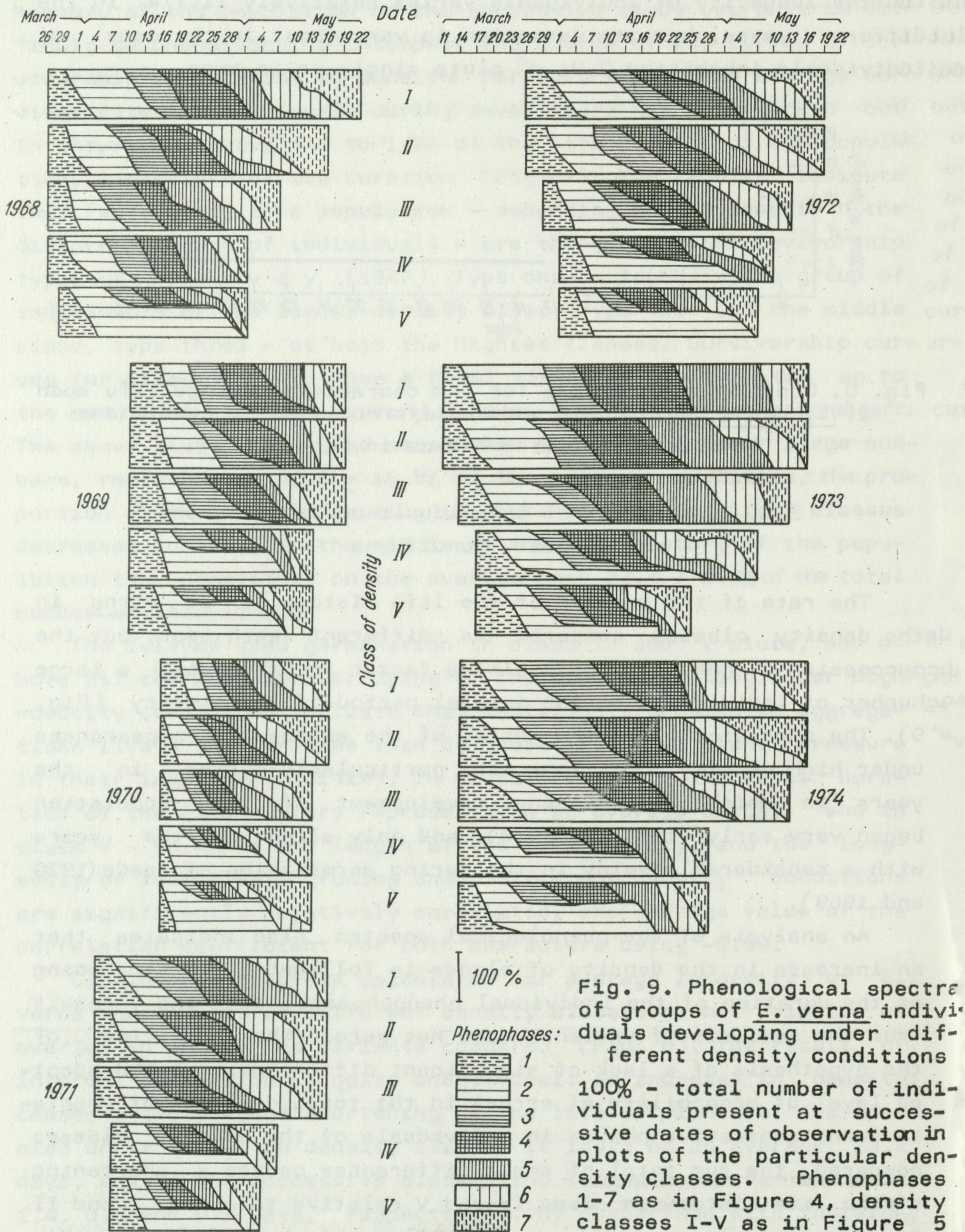
Fig. 8. Confidence intervals for the character: average life span of E. verna individuals under different density conditions

Density classes I-V as in Figure 5

### 3.5. Development of individuals under different density conditions

The rate of the running of the life history of E. verna in the density classes compared is different each year, but the succession of phenophases is always faster in plots with a large number of individuals in the initial period of the history (Fig. 9). The acceleration of the dates of the successive appearances under high density conditions was particularly marked in the years in which the seasonal development of the population began very early (1973 and 1974), and only slight in the years with a considerable delay in the spring germination of seeds (1970 and 1969).

An analysis of the phenological spectra also indicates that an increase in the density of plants is followed by a shortening of the duration of the individual phenophases. Though the result from the analysis of variance does not permit the abolition of the hypothesis of a lack of significant differences (at the adopted level of probability of error) in the total duration of vegetative and generative phases in individuals of the density classes compared, the sum total of small differences causes a shortening of the life history in class IV and V relative to class I and II. It is noticeable in each year, regardless of the weather conditions.



Not all the individuals of a population that have survived the early life stages will attain generative maturity. The development of plants growing in a density of over 35 seedlings per  $0.01 \text{ m}^2$  often stops at an early juvenile stage. In the spectra this is marked by a considerable elongation of the phase of vegetative growth: in class I it lasts in the different years 9-21 days, and in class V 24-39 days. The fraction of these plants is particularly large in class IV and V where it represents over 50% of all the individuals.

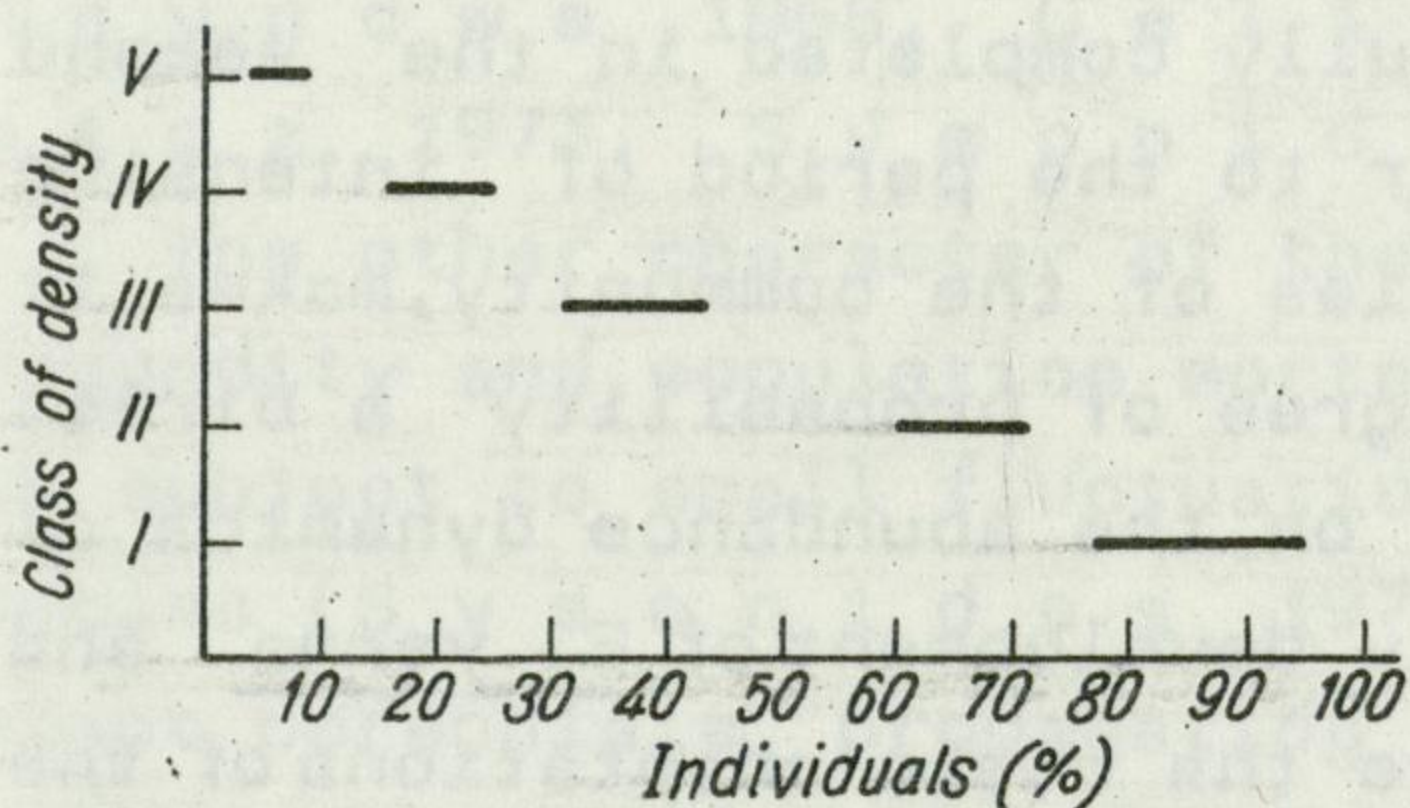


Fig. 10. Confidence intervals for the character: percentage of *E. verna* individuals attaining generative phases under different density conditions. Density classes I-V as in Figure 5

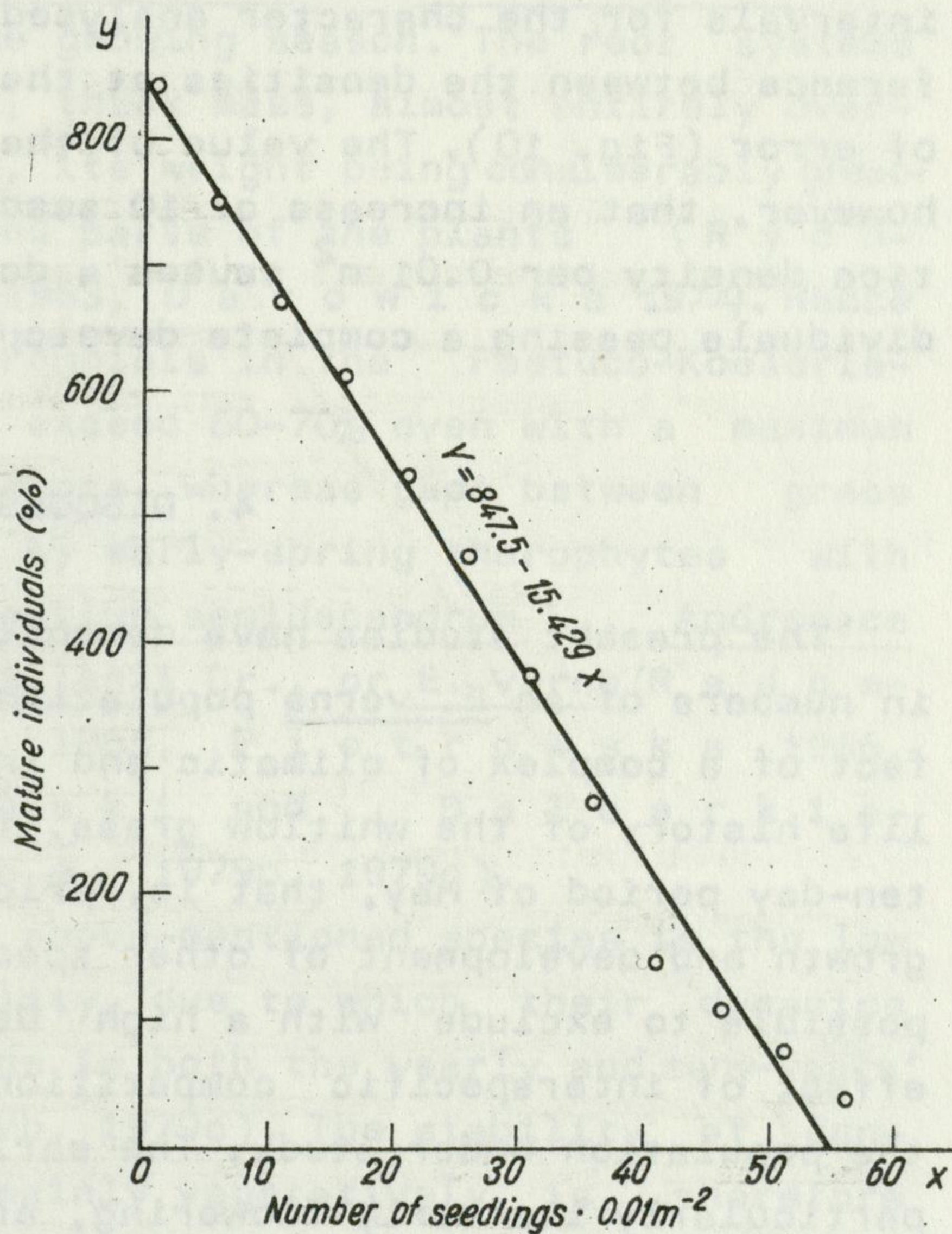


Fig. 11. Relationship between the density of seedlings and the percentage of individuals attaining generative phases in *E. verna* population

A growth of population density is accompanied by a decrease of the percentage of individuals completing their life history. Particularly great differences in this respect were recorded in

1973: the proportions of generatively mature individuals in plots of classes I to V were 100%, 81%, 58%, 27% and only 5%, respectively, of the initial numbers. The least, although significant, differences between the density classes compared were found in 1974 when from 60% individuals in class I to 8% in class V completed their life history. Calculated on the basis of the data for seven years, the average percentage of individuals attaining the fruiting phase in plots of the density classes distinguished ranged from  $85.9 \pm 14.4\%$  in class I to  $7.0 \pm 2.7\%$  in class V. The confidence intervals for the character analysed indicate a significant difference between the densities at the adopted level of probability of error (Fig. 10). The value of the regression coefficient shows, however, that an increase of 10 seedlings in the initial population density per  $0.01 \text{ m}^2$  causes a decrease in the number of individuals passing a complete development by  $15.4 \pm 3.02\%$  (Fig. 11).

#### 4. DISCUSSION

The present studies have demonstrated that seasonal variations in numbers of an E. verna population are the result of the effect of a complex of climatic and intra-population factors. The life history of the whitlow grass, fully completed in the second ten-day period of May, that is, prior to the period of intensive growth and development of other species of the community, makes it possible to exclude with a high degree of probability a direct effect of interspecific competition on the abundance dynamics of the population under study. The early development of E. verna and particularly its early flowering, are the basic adaptations of the species to living in a community of perennials which are, phenologically, much later plants (cf. Turkington and Harper 1979, Ågren and Fagerström 1980, Fagerström and Ågren 1980).

From the above considerations does not follow, however, that E. verna is indifferent to the presence and abundance of perennials. For the latter limit the space within which the population, renewed every year, of the therophyte under study functions. They thus establish the upper limit of abundance which it cannot exceed, at the same time determining its spatial structure. So the number and distribution of the plots colonized in spring by E.



verna seedlings depend directly on the number and distribution of individuals of the other species in a patch (Table I, Figs. 1, 2).

It is for two basic characteristics of the species accompanying E. verna that its population is not entirely eliminated from the community, and the frequency and the general space available to germinating seeds on the whole vary only slightly from year to year. One of the features is connected with the strong development of the roots of psammophyte perennials, especially of individuals of Festuca psammophila, F. duriuscula and Koeleria glauca dominating throughout most of the growing season. The root systems of these plants form a compact, thick mass, almost entirely overgrowing the deeper soil layers, its weight being considerably greater than that of the above-ground parts of the plants (R y c h n o v s k á and K v ě t 1963, D a r o w i c k a 1974). Hence the coverage of the area by perennials in the Festuco-Koelerietum glaucae does not as a rule exceed 60-70% even with a maximum "saturation" of the soil with roots, whereas gaps between grass tussocks may be freely bridged by early-spring therophytes with shallow root systems like: Cerastium semidecandrum L., Androsace septentrionalis L., Veronica dillenii Cr., or E. verna (R a d o m s k i and J a s n o w s k a 1965, P i o t r o w s k a 1966, C e y n o w a 1968, C e l i ŋ s k i and B a l c e r k i e w i c z 1973, S y m o n i d e s 1979b, 1979c).

The other character of the above-mentioned species is the low fecundity and population mortality, due to which their dynamics is subject to small fluctuations in both the yearly and many-years' cycles (S y m o n i d e s 1979b, 1979c). The stability of constant perennials, propagating mainly vegetatively, is therefore the basic determinant of the many-years' stability of numbers also in the therophyte populations. The results of the studies here presented fully confirm this thesis: after the drying up in 1972 of a relatively large number of F. psammophila and F. duriuscula tussocks, the frequency of E. verna seedlings clearly increased, whereas due to an increased fecundity of both grass populations in 1973, the next year already the whitlow grass was found to have retreated from many plots which it had inhabited previously (Fig. 2).

While phytocoenotic relations determine the space available to E. verna population, the weather conditions directly control primarily the date of seed germination, and they have an indirect

effect on the rate of seasonal growth in numbers, and upon the length of the life history (Table II, Figs. 3, 4).

The analysis of the climatic parameters of the period preceding the emergence of the first seedlings suggests that the following were of fundamental importance for the seasonal start of the population of E. verna in the particular years: the date of the disappearance of the snow cover and the air temperature system directly affecting the temperature of the surface soil layers. It is to this group of factors that Solbrig, Newell and Kincaid (1980) attribute the basic role in the initiation and course of the germination of Viola sororia Willd. Meijden and Waals-Kooi (1979) emphasize the importance of soil moisture, and particularly of the interrelationship between the moisture and the temperature of the soil. In their experiments with Senecio jacobaea (L.) they have demonstrated that the higher the soil moisture, the higher the temperature needed for the seeds to germinate, and that a good water supply in the soil considerably shortens the seedling emergence period.

E. verna, an early-spring plant species, can germinate over a fairly wide range of temperatures and moisture, as can other species of plants colonizing unstable or disturbed biotopes (Semenza, Young and Evans 1978, Gross 1980). Each year seedlings emerged several days after the melting of snow and developed irrespective of the weather conditions. It has been found that the germination period was always shorter if germination started at a later date. It is hard to explain this regularity by the effect of any single climatic factor. Probably due to the sum of all the factors on the one hand, and the inner rhythmicity of the species on the other the population attained peak abundance 2-7 days after the appearance of the first seedling (cf. Table II and Fig. 3). Because of the short germination period, the maximum number of seedlings in the area was always equal to the total number of seedlings in the given year.

The weather conditions, and particularly the spring ground frost or a prolonged drought during the juvenile phase of plant development (the seedling and the vegetative growth phases) no doubt contributed to the elimination of a certain number of individuals in the earliest period of their life. Many data indicate that the death risk at the time of becoming independent and of the intensive growth of the young organism is then particularly

great (Hawthorn 1974, Harper 1977, Symonides 1977, Bartolome 1979, Peart 1979, Barkham 1980).

Studies of E. verna have shown, however, that the all-important factor crucial for the survival and development of the individuals is their interactions. Because regardless of the weather conditions in the particular years, the death rate rose with the increasing density of germinated seeds (Figs. 5, 7).

The relationship between the number of seedlings and their survival was the subject of many studies conducted primarily under laboratory conditions, less often in natural systems (Yoda et al. 1963, Palmblad 1968, Symonides 1977, 1978a, Dirzo and Harper 1980, Law 1981, Falencka 1983). The above-quoted papers and many others indicate that the most significant factor reducing the number of seedlings in the population is their overcrowding. It causes a strong "competitive pressure" between individuals of the same age and therefore of similar requirements as regards food and space (Zarzycki 1965, Harkess 1970). The seedlings of E. verna emerge almost simultaneously and do not, therefore, differ much, so the competition for habitat resources appears to have a particularly sharp form as their density increases.

Differences visible throughout the life history of the population in the survival of individuals in plots of the density classes distinguished arise in the early juvenile period and persist until the physiological old age (Fig. 5). A close relationship has in this case been found between the number of seedlings per  $0.01\text{m}^2$  and their survival rate, that is, a significant effect of intra-population interactions on the abundance of the population at an early stage of its development (Fig. 6).

A factor causing a competitive pressure between the fast growing young individuals of E. verna was first of all the lack of sufficiently large, free space (Holt 1972, Ross and Harper 1972). Seedlings that emerged comparatively late, that is, under the rosettes of those that appeared above ground the earliest, probably suffered also because of the lack of a sufficient quantity of light (Kirby 1980). Minor differences in the date of germination may thus give some seedlings the chance to survive and at the same time cause unavoidable death of others (Ross and Harper 1972, Symonides 1978a). During the

exceptionally dry spring of 1974 an additional factor intensifying competition was probably a shortage of moisture in the soil (cf. Barkham 1980, Rahman and Rutter 1980).

In spite of the presence of considerable differences in the survival of seedlings, depending on their density, the total mortality of a population at the early stages of its life is much lower than in many other plant species known in this respect (Cavers and Harper 1967, Marschall and Jain 1969, Matthews and Westlake 1969, Hawthorn and Cavers 1976, Wilkoń-Michałska 1976, Falińska 1977, 1979). The mortality of the seedlings of the population under study is also on the average lower relative to other annual psammophytes found in the study area (Symonides 1974, 1977, 1979b, 1979c).

The relatively low death rate of the early developmental stages in an E. verna population is probably connected with the unusually short life history of the species and its good adaptation to living under variable weather conditions which are unfavourable to plant growth. The relationship between seedling mortality and the length of the life history of the different species has many times been reported in the relevant literature, although the mechanism assuring a better survival for seedlings of ephemeral therophytes relative to plants of a longer life history has not hitherto been fully clarified. It is often attributed to the fact that the life "strategy" of the population of annual plant species differs from that of biennials and perennials (Harper 1967, Harper and Ogden 1970, Putwain and Harper 1970, Mack 1976, Mack and Harper 1977).

After passing the juvenile phase, populations of individuals of many annual species are characterized by a stability of numbers, and often 100% of the survivors attain generative maturity (Sharitz and McCormick 1972, Symonides 1974, 1979b, 1979c). Though in E. verna a lowered death rate can be seen in the middle of the life history of the population, a full equilibrium is rare even in the flowering period. This results from the fact that the growth of the plants, although variable in intensity, occurs at all developmental stages (Symonides 1983). It becomes therefore clear that the demands of individuals for space and food increase in the course of ontogenesis. Thus under the conditions of an overcrowding the negative effects of

the interaction between individuals are not weakened. A relative stabilization in the generative phases can be attained only by groups of individuals living under a low pressure of neighbours from the beginning of their growth (density class I and II), or one resulting from an intensive reduction of seedlings (e.g., in density class IV and V in 1968, 1970 and 1973). However, always in high density classes the stabilization of abundance is very short-lived.

The cause of the gradual dying of individuals almost throughout the life history of the population may also be some permanently acting adverse external conditions: ground frost, too large daily air-temperature amplitudes, droughts and the like. In the last study year it was a long-term spring drought that caused the death of plants regardless of their age and developmental phase. It also caused an intensification of the competitive pressure between individuals: in density class III already only about a dozen per cent of individuals survived till the fruiting phase, in higher density classes - only several (Figs. 5, 9).

As a result of a relatively low mortality of the early juvenile stages and a lack of an equilibrium in numbers, or a weakly marked stabilization in later life periods, the survival of the E. verna population followed type II of D e e v e y ' s (1947) curve - in 1969 and in the years 1971-1974, or was slightly similar to a classical type III curve - in 1968 and 1970. A detailed analysis of the survival of individuals in plots of the particular density classes in the successive years leads to the conclusion that the survivorship curve type is not a character of the species, so it is not associated with its specific "life strategy" (H a r p e r and W h i t e 1974, H a r p e r 1977). Depending on the density of seedlings, their survival in plots of the different classes followed all the classical types, and in the second half of the life history a change in the survival type was found relative to that of the first half (Fig. 7).

Survival according to D e e v e y ' s (1947) type I indicates that individuals practically realize the physiological longevity. It is relatively rare in the world of plants, having so far been recorded for populations of several orchid species (T a m m 1972), Trichachne californica Link. (C a n f i e l d 1957), Carex arenaria L. (N o b l e, B e l l and H a r p e r 1978, S y m o n i d e s 1979b), Poa annua L. (D i r z o and H a r p e r 1980).

In the E. verna population groups of individuals living in a low density (1-2 individuals per plot) followed this type of survival in six consecutive study years, that is, regardless of weather conditions; a considerable decrease in their numbers was only caused by a long-term drought in 1974 in the period preceeding their physiological old age.

The second type of survival, indicating a continual elimination of individuals, regardless of their age and developmental phase, was observed in several species of annuals (Yoda et al. 1963, Symonides 1974, Dirzo and Harper 1980) and in populations of perennials propagating vegetatively (Tamm 1972, Noble, Bell and Harper 1978, Symonides 1979c). It was also this type of survival that E. verna individuals in the intermediate density class usually followed. In spite of a gradual reduction of plants, the requirements of the surviving individuals, increasing with their age, maintained a competitive pressure, which in turn made stabilization of numbers impossible.

The third type of survival is most often represented in natural plant populations (Harper 1977, Bartolome 1979, Symonides 1979a, Gilbert 1980, Gross 1980). Most often the majority of the individuals dying before their physiological old age die already in the seedling phase. This type of survival was represented each year, except 1974, by groups of individuals in plots of the two highest density classes. The competition among the densely crowded seedlings caused their reduction on an average by 53.7% in class IV and as great as 64.7% in class V. The survivors died gradually as in the case of a lower density, nevertheless, the longevity of an average individual in plots of classes IV and V was several times lower (Fig. 8).

The significant shortening of the life span of individuals with an increase in the density of the initial population is caused by both an intensified mortality of the juvenile stages and a faster development of the survivors. A great variation of the life span at a low density suggests that weather conditions are to a large extent superimposed upon genetically determined predisposition. Under the conditions of an overcrowding stress they lose their decisive role in view of the predominating role of the intra-population interactions (Werner 1975, Symonides 1978b).

An analysis of the survival of E. verna individuals under different density conditions shows that the type of the survival of the population is closely related to the spatial structure of the latter. The number and the density of individuals that are subject to a mutual pressure, which varies depending on the distance between them - are the main parameters determining the death rate in the population as a whole, that is, also the course of the seasonal variation in numbers. The period of growth in numbers (seed germination) represents only 5-9% of the total life history of the population, so it has no significant effect on the abundance dynamics over the yearly cycle.

The present studies of E. verna have shown that interactions between individuals have an effect on the course of their phenological development, although climatic factors play a more important role in this respect. As has been stated earlier on, it is the climatic factors that determine the date of germination, closely related with which is the course of the life history and its length. An acceleration of the succession of the consecutive phenophases, as a result of a delayed emergence of seedlings, which has been found during the present studies, was also observed in the populations of several other species of annuals: Spergula vernalis Willd. (S y m o n i d e s 1974), Cerastium semidecandrum, Androsace septentrionalis, Plantago indica L. Trifolium arvense L. (S y m o n i d e s 1978b), Salicornia patula Duval-Jouve (W i l k o ŋ - M i c h a l s k a 1976).

An acceleration of the succession of the consecutive phenophases, a shortening of their duration, and thereby a shortening of the life history of E. verna individuals were also visible as a result of an increase in density, regardless of the weather conditions in the particular years (Fig. 9). At the adopted level of error risk no significant differences have, however, been found in the total duration of the vegetative and generative phases between the density classes of any of the pairs compared. But density has been found to have a significant effect on the fraction of individuals attaining reproductive maturity, that is, completing their ontogenetic development (Figs. 9-11).

This is indicated by the values of the correlation coefficient and of the regression coefficient calculated for the assessment of the average, for the study years, degree of correlation of the two characters (Fig. 11). So if in the group of individuals with

larger distances separating them (class I and II) all individuals surviving early stages flower and fruit (thus on an average  $85.9 \pm 14.4\%$  of the initial population), in plots of the remaining density classes smaller and smaller percentages of individuals attain generative maturity, to as few as  $7.0 \pm 2.7\%$  in class V.

As a result of an increase in the mortality and the concomitant growth of the fraction of individuals failing to attain generative phases with an increasing density - during the seasonal population cycle the proportions of individuals representing the particular density classes change completely. At the level of peak numbers class I individuals represent on an average only  $1.57\%$ , and those of class V -  $36.7\%$  of all seedlings; the proportion of the former among the fruiting individuals is three times bigger, while that of the latter is almost four times smaller.

The study has revealed that a large proportion of individuals in the high density classes pass their life history as stalk-less rosettes of leaves, as juvenile plants. This fact causes a considerable elongation of the vegetative growth phase in heavily overcrowded groups of individuals, regardless of weather conditions. A similar phenomenon was observed in other annuals (Symonides 1978b), and has been known to commonly occur in populations of biennials (Holt 1972, Werner 1975, 1977, Caswell and Werner 1978) and perennials (Rabotnov 1960, Harper and White 1974, Harper 1977, Falínska 1979, Meijden and Waals-Kooi 1979). It appears therefore that a growth in density in an E. verna population on the one hand accelerates the successive phenophases, and on the other hand it completely stops the development of a large fraction of individuals.

An uneven rate of development of individuals in a population, and even within each aggregation, leads on to a gradual differentiation of the population structure. There may occur side by side juvenile, flowering, and even seed-disseminating plants. Under the conditions of a limited space and resources in a biotope a differentiation of individuals is of basic importance for maintaining a relative equilibrium and a comparatively high level of population abundance (Łomnicki 1980). The effect of density on the differentiation of individuals in an E. verna population in respect of the growth rate and size of plants, their habitus and diaspore production will be dealt with in the next paper (Symonides 1983).



## 5. SUMMARY

The present paper is the first of three publications (Symonides 1983, in press) devoted to an analysis of the role of intra-population interactions in the control and regulation of numbers in E. verna. It is concerned with an assessment of the effect of interactions between individuals on the rate of their development and seasonal variations in numbers. This assessment has been made on the assumption that the intensity of interactions between even-aged individuals is the function of the distance separating them, and of the phenological status and size of the plants, and that intra-population relations may to some extent be subject to changing weather conditions.

The study was continued for seven successive growing seasons in four permanent areas, 4 m<sup>2</sup> each, located in a floristically poor patch of Festuco-Koelerietum glaucae (Table I). The areas were divided into square plots 0.1 m in side length. Each day during the seed germination period, and every three days in the later phases of the life history individuals were censused and their phenological development status was determined. On this basis some parameters of the spatial structure of the population were worked out, as well as the course of variations in its abundance and phenological cycle.

In specially selected plots differing in the number of seedlings growing in them, and grouped according to this criterion into five classes, the effect was analysed of density on the survival rate, duration of life history, development rate and percentage of individuals attaining the generative phase.

The study has demonstrated that seasonal variations in numbers in a whitlow grass population are the result of the action of a complex of climatic and intra-population factors. On account of the short life history of E. verna, entirely completed in early spring, that is, before the period of intensive growth of the other plants in the patch, inter-species interactions are not practically involved. However, grass tussocks, especially those of F. psammophila and F. duriuscula, and to a lesser extent also other perennials with strong root-systems determine the overall area available to the small, ephemeral individuals of E. verna, they are therefore one of the factors determining the type of spatial structure of the population (Figs. 1, 2).

Weather conditions directly determine the seed germination date which is closely connected with the disappearance of the snow cover (cf. Table II and Fig. 3). They indirectly determine the duration of the germination period, and thereby the course of the seasonal growth in numbers, as well as the duration of the life history of the population. It has been found that the first seedlings always emerge a few days after the melting of snow, whereas the length of the germination period and of the population life history depends on the date of appearance of the first seedlings, the later the emergence, the longer the periods (Figs. 3, 4).

Depending on the rate of seedling appearance, the seasonal peak of population abundance is observed as early as 2-7 days after the appearance of the first seedling. This period represents only 5-9% of the total duration of the life history of E. verna. The peak level of numbers lasts only about a dozen hours, and the changes that follow it consist exclusively in the elimination of individuals.

The study has revealed a close relationship lasting throughout the study period between the density of seedlings and their survival rate (Fig. 5). The percentage of individuals surviving the consecutive phases of the life history of the population decreases as the density increases. With an increase in density by 1 seedling per  $0.01 \text{ m}^2$ , the death rate rises on an average by  $1.19 \pm 0.2\%$ , whereas significant differences in the mortality of individuals persist also at later life stages (Fig. 6 A, B). Due to this, depending on numbers and on the distances separating individuals, groups of individuals in an E. verna population survive according to type I, II or III of Deevy's (1947) curve, regardless of the date of seedling emergence, length of life history, and to a large extent also irrespective of the weather conditions (Figs. 5, 7). A further consequence of this relationship is a significant differentiation of the life span of an average individual in aggregations of the particular density classes (Fig. 8).

The rate of the course of the life history of E. verna varies from year to year, but the rate of succession of the consecutive phenophases is always faster if density is high. The earlier the beginning of the seasonal development of the population, the more marked this relationship is (Fig. 9). As the density increased, the vegetative growth phase elongated due to the impediment of the development of a number of individuals. The percentage of individ-

uals passing through a complete ontogenetic development is directly dependent on the density of seedlings (Fig. 10). At a density even or greater than 55 seedlings per  $0.01 \text{ m}^2$  only 7% of individuals attain the generative phases. An increase in the initial density by 1 seedling causes a decrease by  $1.4 \pm 0.3\%$  in the fraction of individuals passing a complete life history (Fig. 11).

To sum up, the study has demonstrated that the type of population survival, and thereby also the course of seasonal variations in numbers are closely connected with the spatial structure of the population: number of aggregations and density of individuals under mutual pressure. The same factors also cause a variation of the developmental stages of individuals, leading on to an uneven division of the habitat resources. It is of paramount importance for the maintenance of a relative equilibrium and a comparatively high population abundance (K o m n i c k i 1980).

## 6. POLISH SUMMARY

Praca jest pierwszą z trzech publikacji (S y m o n i d e s 1983, w druku) poświęconych analizie roli oddziaływań wewnątrzpopulacyjnych w ograniczaniu i regulacji liczebności u E. verna. Dotyczy oceny wpływu interakcji między osobnikami na tempo ich rozwoju i sezonowe zmiany liczebności populacji. Ocenę tę przeprowadzono przy założeniu, że intensywność wzajemnych oddziaływań między osobnikami tego samego wieku jest funkcją dzielących je odległości, stanu fenologicznego i rozmiaru roślin, oraz że stosunki wewnątrzpopulacyjne mogą pozostawać do pewnego stopnia pod wpływem zmieniających warunków pogodowych.

Badania prowadzono w ciągu 7 kolejnych sezonów wegetacyjnych na 4 stałych powierzchniach po  $4 \text{ m}^2$ , zlokalizowanych w ubogim florystycznie płacie Festuco-Koelerietum glaucae (tab. I). Powierzchnie podzielono na kwadratowe poletka o boku  $0.1 \text{ m}$ . Codziennie w okresie kiełkowania nasion oraz co 3 dni w późniejszych fazach cyklu liczone osobniki i określano stan ich fenologicznego rozwoju. Na tej podstawie opracowano niektóre parametry struktury przestrzennej populacji oraz przebieg zmian jej liczebności i cyklu fenologicznego.

Na specjalnie dobranych poletkach, zróżnicowanych ze względu na liczbę wyrosłych siewek i pogrupowanych według tego kryterium

na 5 klas, analizowano wpływ zagęszczenia na przeżywanie, długo-  
trwałość cyklu życiowego, tempo rozwoju oraz procent osobników  
osiągających fazy generatywne.

Badania wykazały, że sezonowe zmiany liczebności populacji wio-  
snówki kształtują się w wyniku oddziaływań zespołu czynników kli-  
matycznych i wewnątrzpopulacyjnych. Ze względu na krótki cykl ży-  
ciowy E. verna, zamykający się w całości wczesną wiosną, a więc  
przed okresem intensywnego wzrostu pozostałych roślin w płacie,  
praktycznie nie wchodzi w grę interakcje międzygatunkowe. Silnie  
korzeniące się kępy traw, zwłaszcza F. psammophila i F. duriuscu-  
la, w mniejszym stopniu także inne byliny wyznaczają jednak ogólną  
przestrzeń dostępną dla drobnych, efemerycznych osobników E.  
verna, są więc jednym z czynników określających typ struktury prze-  
strzennej populacji (rys. 1, 2).

Warunki pogodowe decydują bezpośrednio o terminie kiełkowania  
nasion, który jest ściśle związany z topnieniem pokrywy śnieżnej  
(por. tab. II i rys. 3). Pośrednio - wyznaczają długość okre-  
su kiełkowania, zatem przebieg sezonowego wzrostu liczebności, jak  
również długość cyklu życiowego populacji. Okazało się, że  
pierwsze siewki wyrastają zawsze w kilka dni po stopnieniu śniegu,  
zaś okres kiełkowania i cykl życiowy populacji trwają tym krócej,  
im później następuje pojaw siewek (rys. 3, 4).

Zależnie od tempa wyrastania siewek sezonowy szczyt liczebno-  
ści w populacji obserwuje się już po 2-7 dniach licząc od momentu  
pojawienia się pierwszej siewki. Okres ten stanowi zaledwie 5-9%  
całkowitej długości cyklu życiowego E. verna. Stan maksimum  
liczebności utrzymuje się zaledwie kilkanaście godzin, dalsze zmia-  
ny polegają natomiast wyłącznie na eliminacji osobników.

Badania wykazały ścisłą zależność między zagęszczeniem siewek  
a ich przeżywaniem, występującą w całym okresie badań (rys. 5).  
Procent osobników przeżywających kolejne fazy cyklu życiowego po-  
pulacji zmniejsza się wraz ze wzrostem zagęszczenia. Śmiertelność  
siewek rośnie przeciętnie o  $1,19 \pm 0,2\%$  przy wzroście zagęszcze-  
nia o 1 siewkę na powierzchni  $0,01 \text{ m}^2$ , zaś istotne różnice w śmier-  
telności osobników utrzymują się także w późniejszych etapach ży-  
cia (rys. 6 A, B). Powoduje to, że grupy osobników w populacji E.  
verna, zależnie od ich liczebności i odległości między osobnika-  
mi, przeżywają zgodnie z typem I, II lub III krzywej  $D e e v e -$   
 $y ' a$  (1947), bez względu na termin pojawu siewek, długość  
cyklu życiowego, a w dużym stopniu także niezależnie od warunków

pogodowych (rys. 5, 7). Dalszą konsekwencją tej zależności jest istotne różnicowanie długości życia przeciętnego osobnika w skupiskach poszczególnych klas zagęszczeń (rys. 8).

Tempo przebiegu cyklu życiowego E. verna jest różne w różnych latach, zawsze jednak następstwo kolejnych fenofaz jest szybsze w warunkach dużego zagęszczenia. Zjawisko to jest tym wyraźniejsze, im wcześniej rozpoczyna się sezonowy rozwój populacji (rys. 9). W miarę wzrostu zagęszczenia stwierdzono także wydłużanie się fazy wzrostu wegetatywnego, spowodowane zahamowaniem rozwoju pewnej liczby osobników. Procent osobników przechodzących pełny cykl ontogenetyczny jest ściśle związany z zagęszczeniem siewek (rys. 10). Przy zagęszczeniu równym lub przekraczającym 55 siewek na powierzchni  $0.01 \text{ m}^2$  zaledwie 7% osobników osiąga fazy generatywne. Wzrost zagęszczenia początkowego o 1 siewkę powoduje spadek frakcji osobników odbywających pełny cykl o  $1.4 \pm 0.3\%$  (rys. 11).

Reasumując, badania wykazały, że typ przeżywalności populacji, a więc i przebieg sezonowych zmian liczebności są ściśle związane ze strukturą przestrzenną: liczbą skupisk i zagęszczeniem osobników podlegających wzajemnej presji. Od tych czynników uzależnione jest także różnicowanie stanu rozwojowego poszczególnych osobników, prowadzące do nierównego podziału zasobów środowiska. Ma ono podstawowe znaczenie dla utrzymania względnej równowagi i stosunkowo dużej liczebności populacji (Ł o m n i c k i 1980).

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