

EKOLOGIA POLSKA (Ekol. pol.)	32	4	557-580	1984
---	-----------	----------	----------------	-------------

Ewa SYMONIDES

Department of Phytosociology and Plant Ecology, Institute of Botany,
Warsaw University, Al. Ujazdowskie 4, 00-478 Warsaw, Poland

**POPULATION SIZE REGULATION AS A RESULT
OF INTRA-POPULATION INTERACTIONS
III. EFFECT OF *EROPHILA VERNA* (L.)
C. A. M. POPULATION DENSITY ON THE ABUNDANCE
OF THE NEW GENERATION OF SEEDLINGS.
SUMMING-UP CONCLUSIONS**

ABSTRACT: The dynamics was studied of natural aggregations of *Erophila verna* individuals and the seed germination capacity under laboratory conditions. A significant, negative correlation has been found between the number of seedlings and of adult individuals in the particular year, and the number of seedlings the next year, and a positive correlation between the number of seeds in the soil and the number of individuals of the new generation. It has been demonstrated that the numerical equilibrium of the population over a many-years' cycle is determined by natality differences among the aggregations of individuals.

KEY WORDS: *Erophila verna*, seed production, germination capacity of seeds, density-dependent reproduction of individuals, many years' population abundance dynamics.

C o n t e n t s

1. Introduction
2. Material and methods
3. Results
 - 3.1. Factors determining seed germination and number of seedlings under natural conditions
 - 3.2. Germination capacity of seeds and their longevity under laboratory conditions
 - 3.3. Role of diversified individual reproduction in the regulation of population abundance
4. Discussion
5. Summing-up conclusions
6. Summary
7. Polish summary
8. References

1. INTRODUCTION

Studies of the population dynamics of therophytes have demonstrated that, regardless of the ecosystem type, variations in the number of seedlings in the successive years are usually far narrower than variations in the total number of seeds produced in a population, annuals realizing their reproductive potential only to a small extent (Went 1973, Symonides 1974a, 1974b, Wilkoń-Michalska 1976, Falińska 1979). The lack of a close relationship between the production of seeds and the number of individuals in the new generation suggests that the natality of a therophyte population is mainly determined by biotope and/or biocoenotic, and not intra-population factors (Raynal and Bazzaz 1975, Inouye, Byers and Brown 1980, Grubb, Kelly and Mitchley 1982). Influenced by the latter is the magnitude of mortality, most often positively correlated with the density of the seedling population (Palmbald 1968, Symonides 1974c, 1977, Law 1981, Falencik 1983). If the density of seedlings is determined by properties of the external environment, then consequently, these should be attributed a crucial, though only indirect, role also in the course of the dying of individuals.

The above considerations make one inclined to formulate the following hypotheses: (1) the many-years' and seasonal therophyte abundance dynamics is the result primarily of the effect of external factors on the population; (2) inter-individual interactions can only cause a reduction in the initial population abundance to the level of the carrying capacity of the biotope; (3) in therophytes intra-population relations are characterized by a time discontinuity; their effects affect only one generation of individuals; (4) the magnitude of natality — provided a sufficiently large number of seeds reach the soil — is independent of the population density in the preceding year.

Is the role of inter-individual interactions among therophytes really reduced solely to the limiting of the population size? The results from several-years' research into the population dynamics of *Erophila verna* have shown that it would be purposeful to verify the above hypotheses. For it has been found that although the total number of individuals in the population varies slightly in the analogous periods of the growing season from year to year, in different places of the biochore the emergence of seedlings was — alternately — very abundant or very scanty (Symonides 1983a). The repeatability of the phenomenon suggests the functioning in *E. verna* of some, hitherto little-known, mechanisms of intra-population regulation of numbers, and imposes the necessity to take into account the spatial relations among individuals in population dynamics studies.

The aim of the studies presented in this paper was to clarify the causes, as well as the results of the yearly variations in the number of seedlings at different points of the population area of *E. verna*. The following assumption has been adopted as a point of departure: if the number of seedlings emerged in a given place is negatively correlated

with the number of seedlings in the next year, then there occurs a regulation phenomenon in that population, and not only an abundance-limiting mechanism. This at the same time proves the falseness of the hypothesis assuming a lack of continuity of the effects of intra-population interactions in successive generations.

The research was restricted to those natural aggregations of individuals for which the highest density values in the seedling phase were found. In such aggregations analysed were the production of seeds, number and fraction of seeds getting into the soil, and the number of seedlings of the new generation. In the laboratory, seeds were tested for the capacity and speed of germination, and their weight and longevity were determined. Thus the scope of study included measurement of the reproduction of spatially separated aggregations of individuals differing in initial density, and an analysis of the factors responsible for the magnitude of this reproduction. Apart from this, the role has been assessed of differences in natality among aggregations in determining the many-years' population dynamics as a whole.

The present paper is the last part of a wide-scope series of studies on variations in *E. verna* population abundance under natural conditions, aimed at an assessment, as full as possible, of the role of inter-individual interactions in the determination of seasonal and many-years' population dynamics. Two earlier publications dealt with the effect of intra-population interactions on the survival rate, growth rate, development rate, and the size and fecundity of individuals (Symonides 1983a, 1983b).

2. MATERIAL AND METHODS

Field investigations were carried out in the years 1973–1976 in a patch of *Festuco-Koelerietum glaucae* Klika 1931, near permanent areas, where the survival and development of *E. verna* individuals were followed (Symonides 1983a). Early in the spring of 1973 two series of plots were laid out, each of the size 0.01 m², spatially separated from each other (by a distance of 0.9–1.2 m): 130 plots with 1–4 seedlings and 130 plots with 50–60 seedlings each. All plots were located at flat sites, devoid of plants of other species, in the vicinity of large tussocks of *Festuca duriuscula* L., *F. psammophila* (Haeckel) Krajina, and *Koeleria glauca* (Schkuhr) DC.

Every year in 10 permanent plots of each series all adult individuals were counted, the production of seeds was estimated, and the following spring the seedlings were counted. The data thus obtained were used for the assessment of the natality of the particular aggregations of individuals, and evaluation of the interrelationship between the number of seedlings, number of adult individuals and the number of seeds produced in the particular year, and the number of seedlings in the next generation. In the assessment of the seed production in individual plots the results were used of studies of the fecundity of individuals that had grown under different density conditions

(Symonides 1983b). The adopted measure of natality was the number of seedlings per an adult individual in the preceding year. On the termination of the germination phase in 1976 *E. verna* seeds contained in 1 cm soil layer of each plot were counted.

Immediately after the termination of the seed dissemination phase from twenty other plots of each density class the above-ground parts of plants were removed, and the top soil layer 1 cm thick was cut off. In the laboratory, the surface area of the leaf rosettes was measured by means of a planimeter, and the soil was dried and screened, whereafter the whitlow-grass seeds were picked out and counted. In the subsequent two years, successive plots, 10 of each of the two series laid out in the first study year, were used for a similar analysis. A number of quantities, ratios and relationships have been calculated: the size of the area of each plot not covered by *E. verna* leaf rosettes, percentage of the seeds that got into the soil relative to the number of seeds produced, then the type and degree of interrelationship between seed production and seed number in the top soil layer, and between the size of the area not overgrown and the number of seeds that got into the soil.

From individuals growing in the remaining plots ripe silicles were picked and seeds were dissected out. Every year seeds were harvested of plants from 30 plots of one series and 30 plots of the other series. Part of the seeds were kept in paper envelopes and part were put in cloth bags which were then buried in small flower pots filled with soil. The envelopes and flower pots, marked appropriately, were kept at room temperature (18 – 21°C) until the end of October each year, then – until the end of February – at 5 – 6°C; the soil moisture in the flower pots was maintained at the level of 5 – 7% actual moisture. In the analysis of seed germination capacity and longevity seeds from individuals growing under low and high density conditions, kept “dry” in envelopes, and in soil were considered separately.

In the analysis of seed germination capacity three sowing variations and three replications of each variant were used. In each case a 100-seed random sample was handled. Every year in March seeds were sown on moistened filter paper placed in Petri dishes, into soil at a depth of 0.3 cm, and into soil at a depth of 2 cm; cuvettes containing soil were watered every day with the same amount of water. Germs were counted every 24 hours for 10 days.

For the seed longevity studies seeds harvested in 1973 and 1974 were used. A random 100-seed sample was sown every year in March onto filter paper, using three replications in each case. This series was continued until 1982.

In 1975, once only, the mean weight was determined of 1000 seeds derived from plants growing under low and high density conditions. The seeds were dried at 110°C for 48 hours and weighed with an accuracy of 0.0001 g. The mean weight of seeds has been calculated on the basis of three replications, and the significance of differences has been established after taking into account confidence semi-intervals.

In all the statistical analyses a 5% error risk was adopted. Studies of the interrelationships between the different pairs of characters were carried out separately for the data from plots with a low and from those with a high seedling density.

3. RESULTS

3.1. FACTORS DETERMINING SEED GERMINATION AND NUMBER OF SEEDLINGS UNDER NATURAL CONDITIONS

Average seedling density in the plots of both series changes regularly from year to year, attaining — alternately — very high and very low values. Subject to regular variations also is the density of adult individuals, although in this case the fluctuations are considerably smaller: while during the seedling phase there is on an average a 25- up to 30-fold increase or decrease in the number of individuals on the surface of a plot between successive years, there can only be a 5-fold growth or decrease during the fruiting phase (Fig. 1).

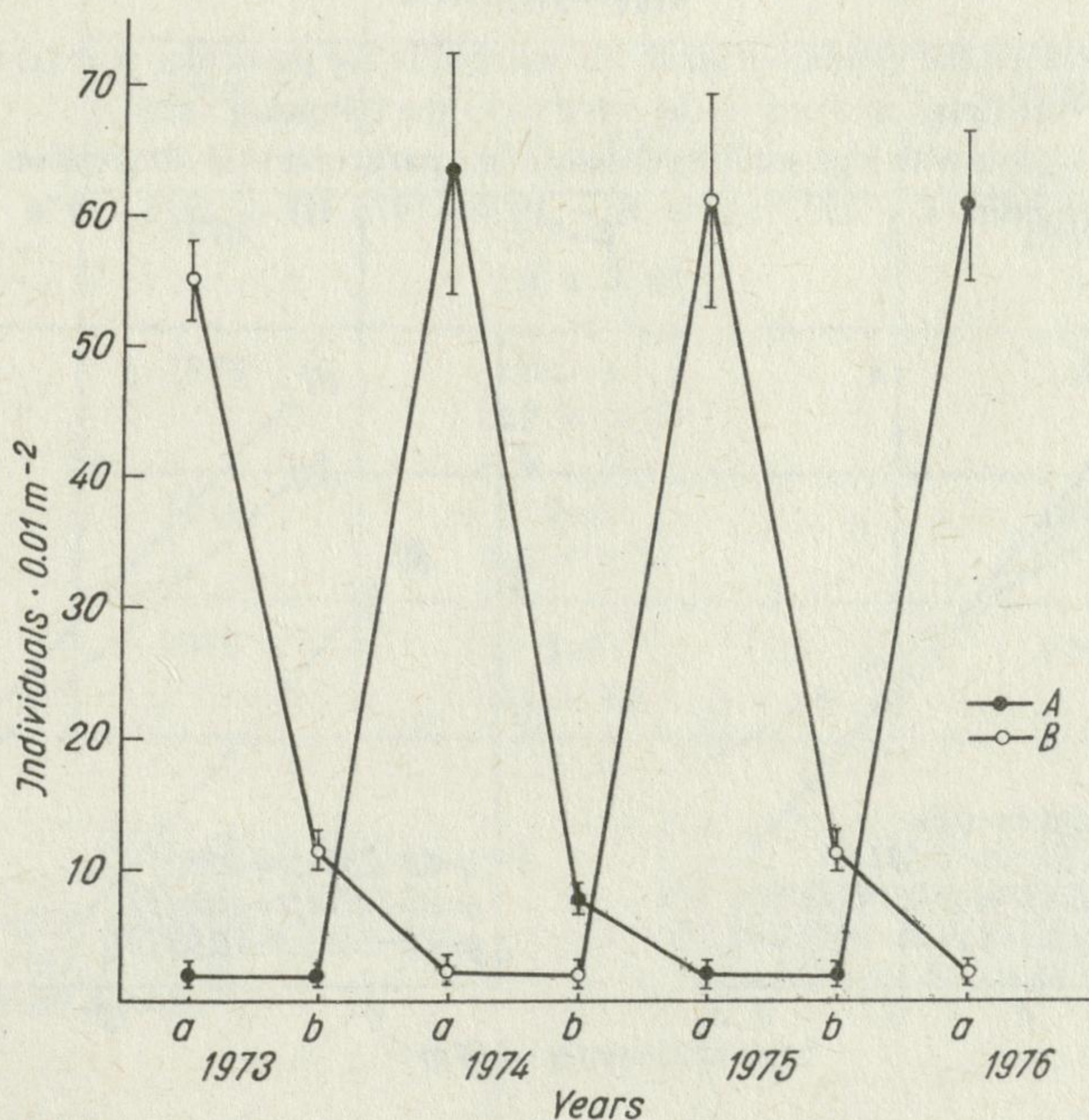


Fig. 1. Changes in the number of individuals in plots with low (A) and high (B) seedling density in the first study year

a — seedling phase, b — fruiting phase

The number of seedlings that emerged in the different plots in the particular year is closely, negatively correlated with the number of seedlings covering the same plots in the following year, the value of the correlation coefficient ranging from $r = -0.87$ to $r = -0.96$ (Fig. 2). In plots of both series the number of seedlings is also significantly, negatively correlated with the total number of those individuals that survived until the fruiting and seed dissemination phases in the preceding generation (Fig. 3).

At the level of the adopted error risk no significant relationship has been found between the production of seeds, as estimated in relation to the surface area of a plot,

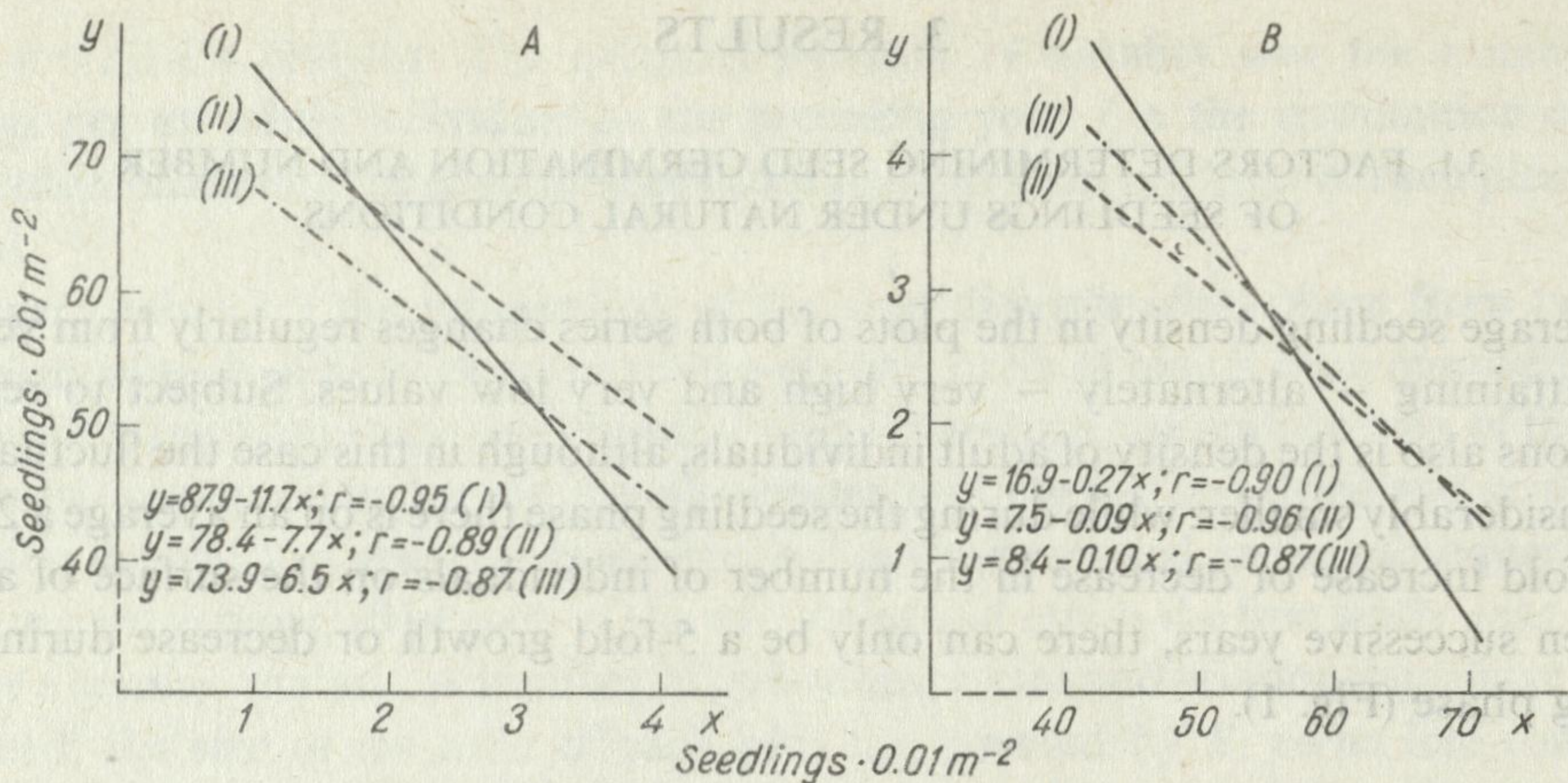


Fig. 2. Relationship between the number of seedlings emerged in the particular year (x) and the number of seedlings emerged in the same plots the following year (y)

A — plots with low, B — plots with high seedling density in the particular year. Regression lines for successive year pairs: I — 1973—1974, II — 1974—1975, III — 1975—1976

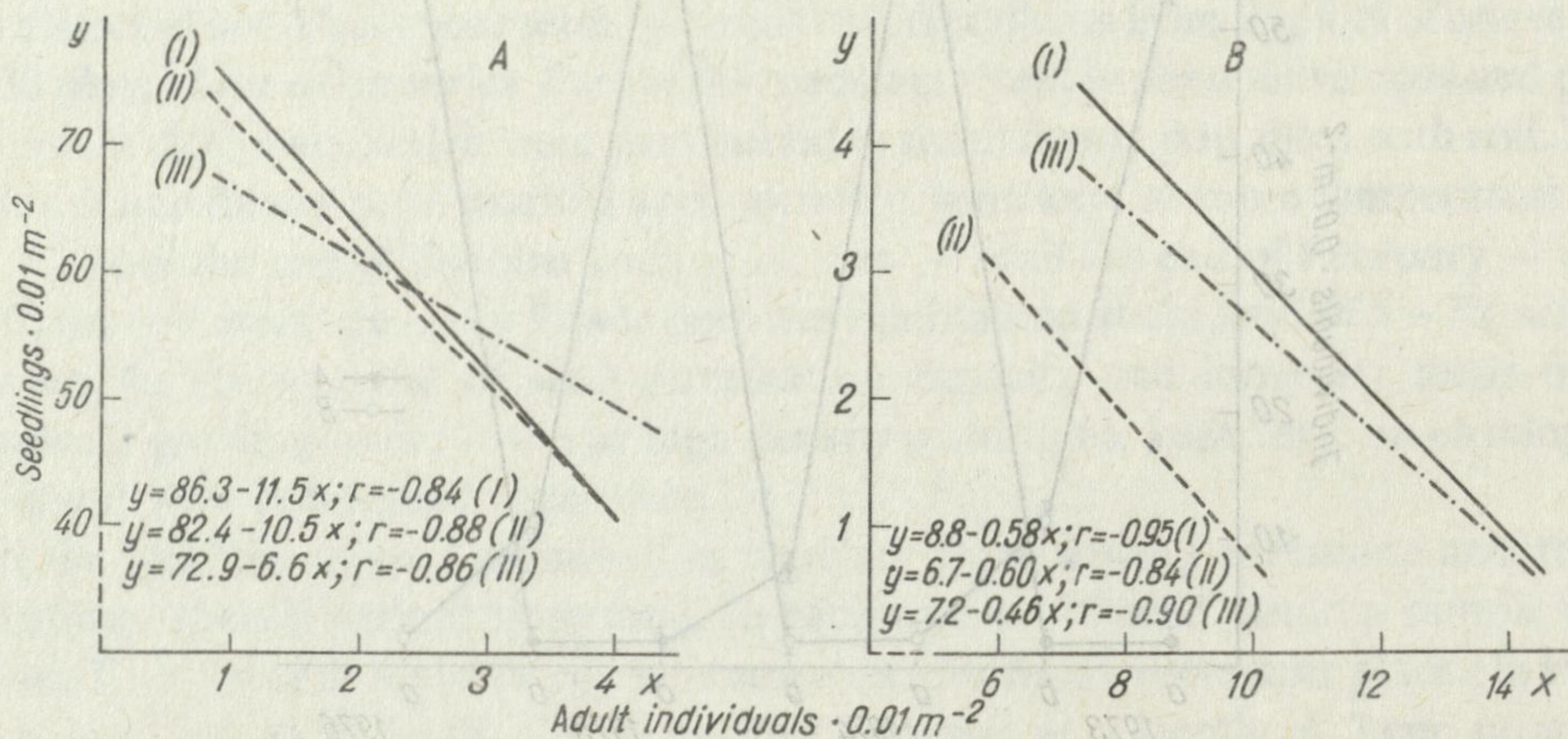


Fig. 3. Relationship between the number of adult individuals in plots in the particular year (x) and the number of seedlings emerged in the same plots the following year (y)

Explanations — as for Figure 2

and the number of seedlings found next year. Such a correlation can only be found if data from one series and those from the other are treated jointly during the study period ($r = 0.81$). The above-quoted results thus prove that there is a continuity of intra-population interaction between successive generations, but at the same time they indicate that there are factors, more significant than the magnitude of seed production, responsible for the regulation of population abundance over a many-years' cycle.

The total number of seeds produced by individuals that grew under low density conditions is every year several times larger than that found for strongly compact

aggregations. In either case seed production differs between years, but it is always much higher than the number of seedlings in the next growing season. Differences in seed production between plots of one series and those of the other are each year very big, and they result primarily from differences in the number of fruiting individuals (Table I).

Table I. Number of fruiting individuals and the total seed production in plots with a low and high density in the seedling phase (plot size 0.01 m²)

Seedling density	Year	Number of fruiting individuals (min.-max. $\bar{x} \pm \sigma$)	Seed production ($\bar{x} \pm \sigma$)
Low	1973	1-3 2.0 \pm 0.66	2180.2 \pm 680.7
	1974	1-4 2.0 \pm 0.67	1143.3 \pm 150.9
	1975	1-3 1.8 \pm 0.79	1984.2 \pm 465.4
High	1973	2-4 2.9 \pm 0.88	233.9 \pm 86.3
	1974	5-7 6.0 \pm 0.66	141.3 \pm 15.3
	1975	2-5 3.7 \pm 1.1	319.6 \pm 77.4

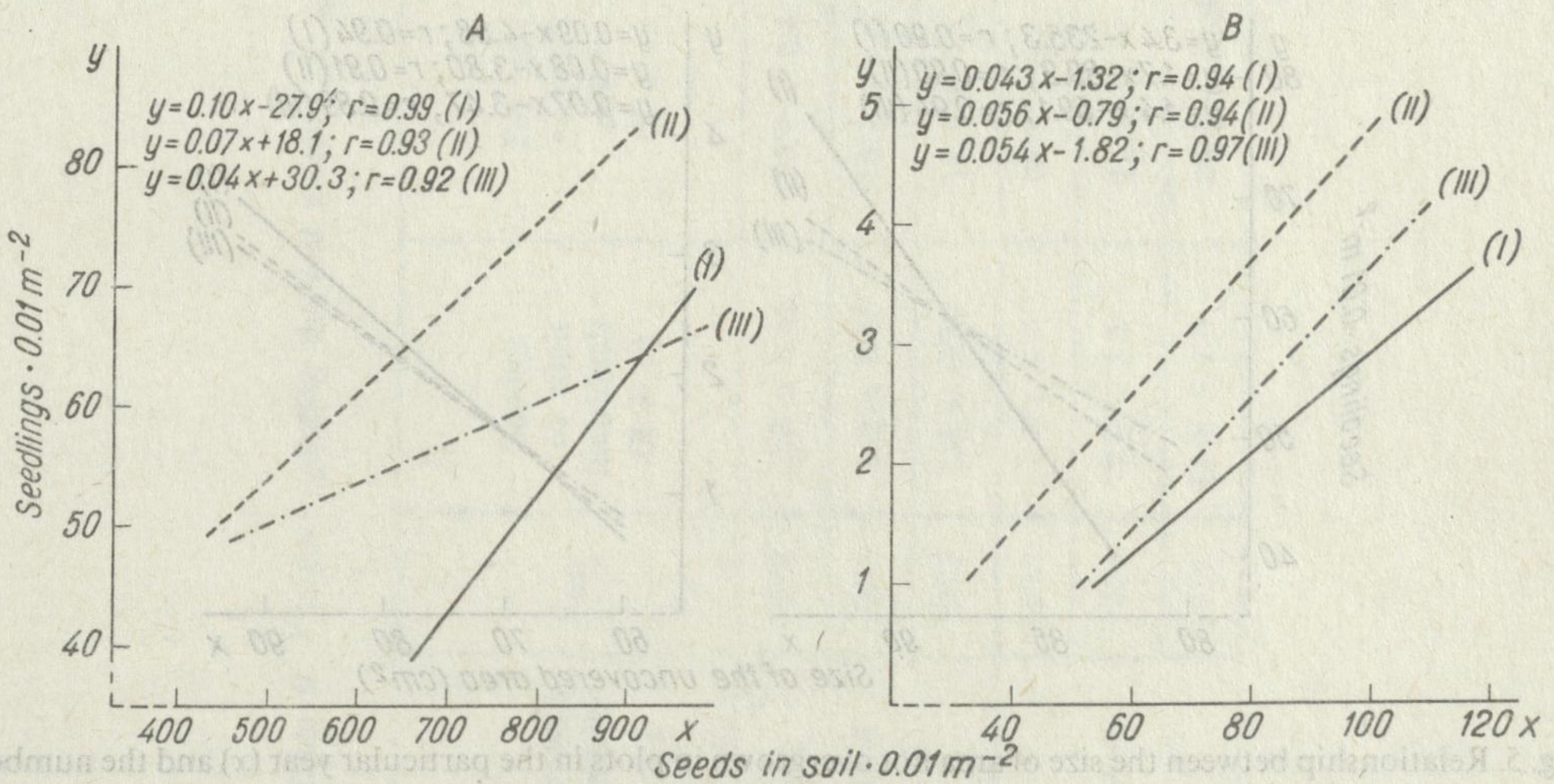


Fig. 4. Relationship between the number of seeds in the surface soil layer in the particular year (x) and the number of seedlings growing in the same plots the following year (y)

Explanations as for Figure 2

In different years from 13.2 to 89.1% of the overall pool of seeds produced in the particular plots get into the soil. Although the variability of the character under study is great, a significant, almost linear relationship has been found between the number of seeds found in the surface soil layer of the different plots and the number of seedlings that emerged in the next growing season in plots with an analogous density of individuals during the seed dissemination phase of the previous year (Fig. 4).

From the statistical point of view, the relationship between the number of seeds in the surface soil layer and the number of seeds produced in the same unit area is equivocal; the value of the correlation coefficient over the range of the two density classes considered varied very widely in the particular years: from $r = 0.80$ to $r = -0.66$. If, however, a statistical sample consists of the mean values of the two

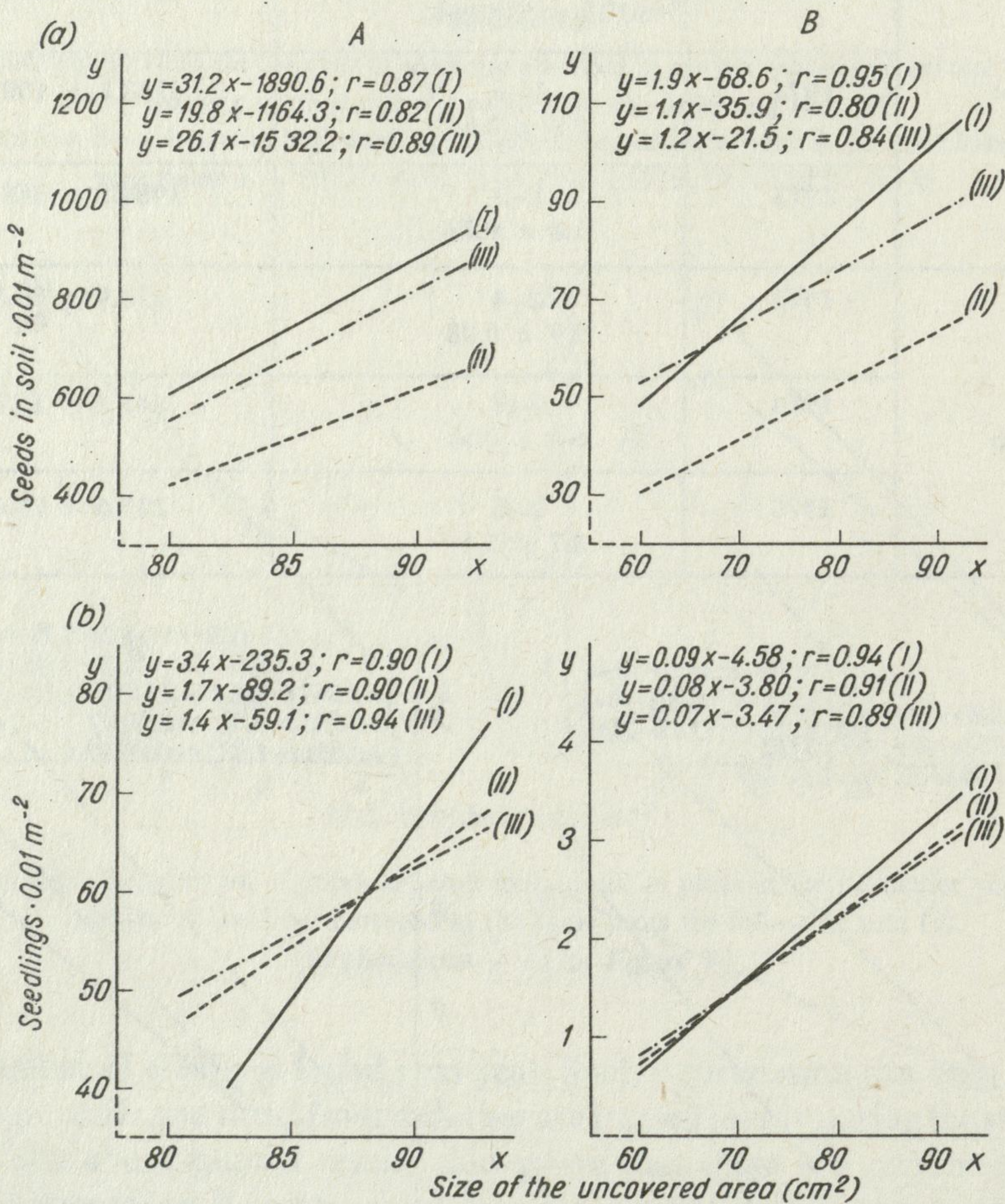


Fig. 5. Relationship between the size of area not overgrown in plots in the particular year (x) and the number of seeds getting into the soil (y), and the number of seedlings emerging in plots of the same density the following year (y)

Regression lines: (a) I — 1973, II — 1974, III — 1975, (b) I — 1973—1974, II — 1974—1975, III — 1975—1976; other explanations as for Figure 2

Table II. Factors regulating the real natality of aggregations of individuals in plots with a low and high density in the seedling phase (plot size 0.01 m²)

Seedling density	Year	Number of adult individuals ($\bar{x} \pm \sigma$)	Per cent cover of surface ($\bar{x} \pm \sigma$)	Seeds in surface soil layer			Natality ($\bar{x} \pm \sigma$)
				number ($\bar{x} \pm \sigma$)	percentage of seeds produced ($\bar{x} \pm \sigma$)	percentage of seeds germinating next year ($\bar{x} \pm \sigma$)	
Low	1973	2.0 ± 0.66	10.9 ± 2.4	889.1 ± 87.9	46.8 ± 22.9	7.1 ± 0.34	37.4 ± 20.4
	1974	2.0 ± 0.66	10.7 ± 4.3	605.2 ± 103.1	54.4 ± 14.6	10.2 ± 0.57	35.8 ± 20.5
	1975	1.8 ± 0.79	10.7 ± 4.1	794.3 ± 125.2	43.6 ± 17.7	7.8 ± 0.77	37.8 ± 20.9
High	1973	11.4 ± 1.5	21.5 ± 9.1	82.7 ± 20.1	37.1 ± 8.1	2.6 ± 0.52	0.21 ± 0.11
	1974	7.8 ± 1.1	21.5 ± 9.2	49.5 ± 13.7	35.1 ± 9.4	3.9 ± 0.78	0.28 ± 0.15
	1975	11.4 ± 1.8	23.5 ± 11.8	70.0 ± 16.8	24.4 ± 13.2	2.7 ± 0.68	0.19 ± 0.11

characters, computed on the basis of data from 10 plots of one series and 10 plots of the other series, in three consecutive years, the correlation coefficient takes a positive sign and attains a value close to unity ($r = 0.98$).

Further analyses of the data have shown that the factor determining the fraction of seeds getting into the soil in the different plots is the size of the surface area not covered with whitlow-grass leaf rosettes. This points to a positive relationship between the surface area accessible to the seeds shed and their number in the soil determined immediately after the termination of the dissemination, this relationship being significant for both density series of each year (Fig. 5 a). As a result of this relationship, there is a correlation also between two other characters: the size of the area not overgrown and the number of seedlings in the next generation (Fig. 5 b).

The size of the area not covered by leaf rosettes of adult *E. verna* individuals in plots of both series changes from year to year in a direction opposite to the direction of changes in the number of individuals surviving till the fruiting and seed dissemination phases (Table II). Each year the coverage of the surface by the leaf rosettes of more compact aggregations of individuals is 10.6–12.8% higher than the joint coverage in plots with a low density. No wonder the proportion of seeds that get into the soil, relative to the total number of seeds produced within highly compact aggregations, is on an average over a dozen per cent smaller than in sparsely overgrown places (Table II).

A comparison of the ratio of the number of seeds in the surface soil layer to the number of seedlings emerging in spring in the different plots in the successive years indicates that under natural conditions an average of 5.7% of seeds germinate. An almost three times higher percentage of germinating seeds in plots with a low density of individuals in the preceding year than in high-density plots is a regularity (Table II). At the same time the variation of the germinating fraction in the plots of the density series compared each year is found to be characteristically very narrow; the average variation coefficient value is 6.04% and does not exceed 14.8%.

Calculated for the particular aggregations of individuals, natality is on an average 161 times higher in plots with a low initial density than in those with a high density, and varies relatively little from year to year in aggregations of the same density class. Its value is not directly related to the number of seeds in the surface soil layer; the number of seeds varied conspicuously during the study period, differences between successive years being proportionately greater in high-density plots (Table II). It must be noted, however, that at the most only a few (from 0 to 11 in the different samples) seeds are found in the surface soil layer at the end of the germinating and seedling establishing period, with no significant differences found in this respect between plots of the density classes compared.

3.2. GERMINATION CAPACITY OF SEEDS AND THEIR LONGEVITY UNDER LABORATORY CONDITIONS

The germination capacity of *E. verna* seeds under laboratory conditions is many times as high as under natural conditions, and is insignificantly variable between years

Table III. Germination of seeds from individuals growing in plots with a low and high density in the seedling phase

a — seeds stored in envelopes, sown onto filter paper; b — seeds stored in envelopes, sown into soil; c — seeds stored in soil, sown onto filter paper; d — seeds stored in soil, sown into soil

Seedling density	Year	Per cent germination ($\bar{x} \pm \delta$)			
		a	b	c	d
Low	1973	52.3 \pm 1.5	41.3 \pm 1.5	42.0 \pm 1.0	35.7 \pm 1.5
	1974	50.8 \pm 1.3	40.7 \pm 1.2	40.9 \pm 0.9	34.3 \pm 1.4
	1975	52.9 \pm 1.5	42.0 \pm 1.5	42.7 \pm 1.1	36.2 \pm 1.5
High	1973	36.3 \pm 0.58	27.0 \pm 1.0	26.7 \pm 1.1	24.0 \pm 1.0
	1974	35.4 \pm 0.47	26.1 \pm 0.9	25.8 \pm 1.0	23.7 \pm 0.9
	1975	37.2 \pm 0.61	27.9 \pm 1.1	27.2 \pm 1.2	24.9 \pm 1.2

if analogous experimental schemes are compared (Table III). The total number of germinated seeds, as well as the course of the germination depend on the density at which the parent plants grew, conditions under which the seeds were stored prior to their sowing, and the substrate type and depth of sowing.

The highest per cent germination is found for seeds of low density individuals, kept "dry" in envelopes and sown onto wet filter paper. Seeds derived from highly crowded aggregations, stored in flower pots containing soil, and sown at a depth of 0.3 cm in soil-filled cuvettes are characterized by a per cent germination that is over a half lower. Seeds sown at greater depths, under a 2 cm soil layer, do not germinate at all, regardless of the conditions under which the parent plants grew, and the manner of their storage after harvesting.

From Table III follows that the number of germs emerged from seeds depends to a larger extent on the density of parent plants than on the storage conditions or kind of substrate onto which the seeds were sown. Conversely, the course of germination is affected in a decisive way by the latter two factors, while the density of parent plants does not play an important role (Fig. 6).

Germs of seeds stored in soil-containing flower pots and sown onto wet filter paper begin to emerge as early as about a dozen hours after sowing, peak germination occurs on the second day, and the germination process ceases completely after 72 hours. The germination of a seed sample stored in a similar way lasted only 96 hours when the seeds had been sown into the surface soil layer. In this case, however, the first germs appeared only on the second day after sowing, but a day later the peak germination already occurred. Much less intensive, spread over the whole week, was the course of germination of the seeds stored in envelopes and sown onto filter paper (Fig. 6).

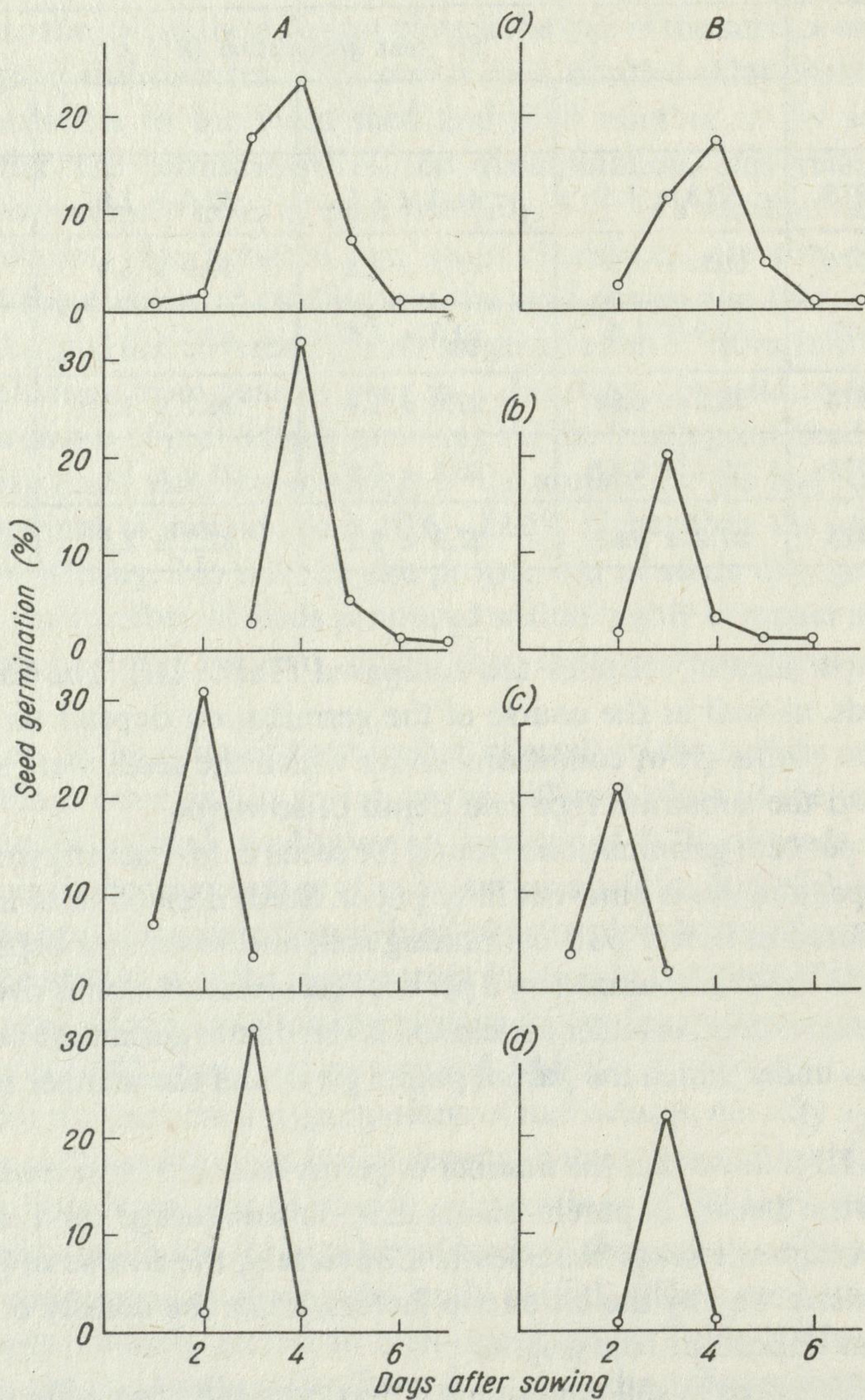


Fig. 6. Course of germination of seeds of individuals developed at low (A) and high (B) seedling density a — seeds stored in envelopes sown onto filter paper; B — seeds stored in envelopes, sown into soil; c — seeds stored in soil, sown onto filter paper; d — seeds stored in soil, sown into soil

By contrast to the germinating capability, the longevity of seeds is independent of the density of the parent plants; nor did seeds collected in 1973 and 1974 significantly differ in longevity. There is, however, a significant influence of the storage conditions on the maintenance of the germinating capability for a long time. Though seeds stored "dry" in envelopes germinate most intensively 10 months after being harvested (i.e., in the next growing season), whereafter their viability gradually drops, a small proportion of them still germinate after eight years. In the soil environment, already in the second year following the harvest a small percentage of seeds germinate, and few of them remain viable for 3–4 years (Fig. 7).

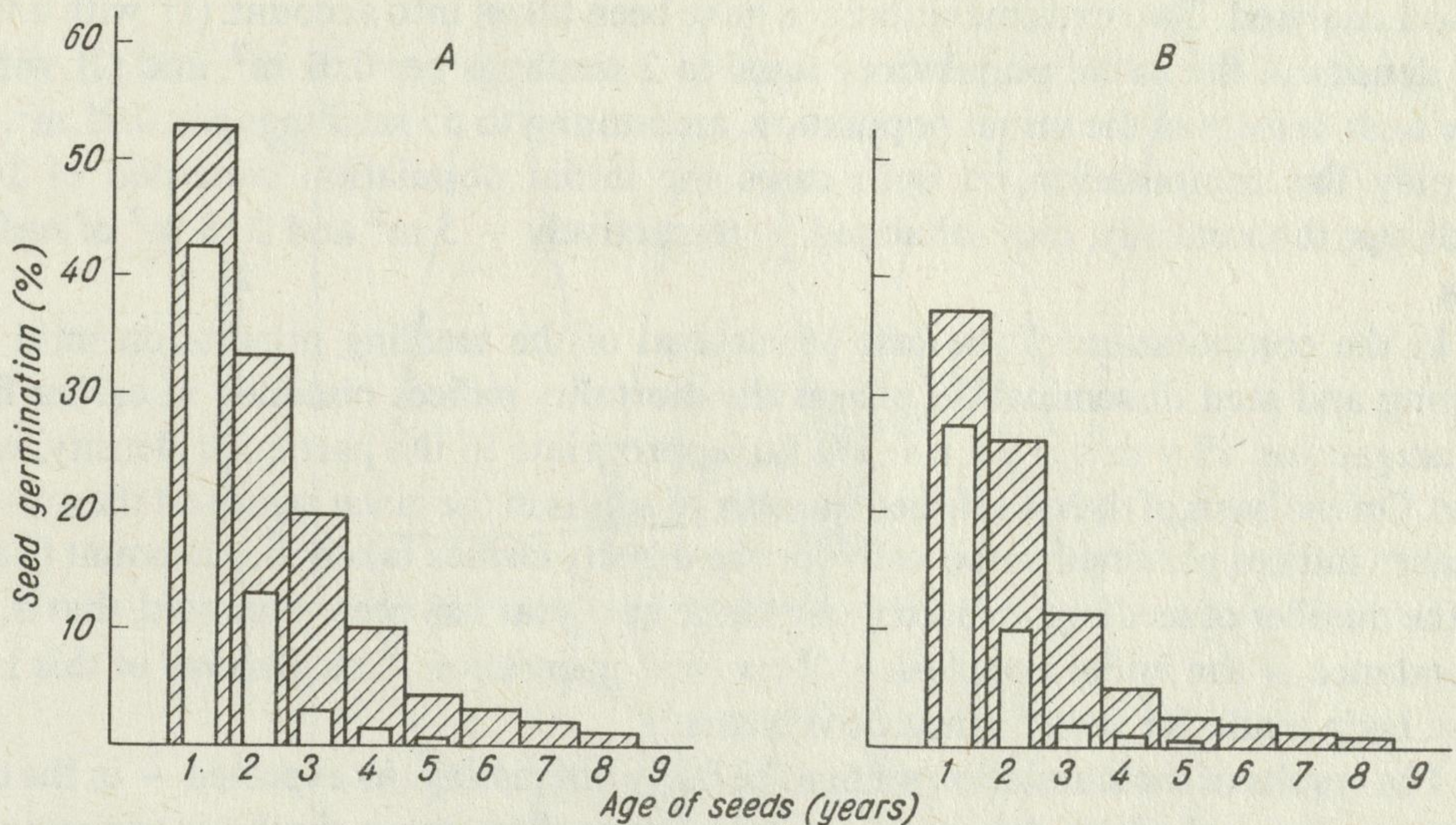


Fig. 7. Germination capacity and longevity of seeds of individuals grown at low (A) and high (B) seedling density

dark columns — seeds stored "dry" in envelopes, light columns — seeds stored in moist soil

The weight of one thousand seeds from individuals that grew under low density conditions is — at the level of the adopted error risk — significantly higher than the weight of one thousand seeds from individuals which grew in highly compact aggregations. The value of the mean and of the confidence semi-intervals, expressed in milligrams, is $0.086 < 33.24 < 0.086$ in the former case, and $0.18 < 28.13 < 0.18$ in the latter case. A comparison of the values quoted shows that the variation of the character studied is greater when plants grow in aggregations than when they grow singly or at a low density.

3.3. ROLE OF DIVERSIFIED INDIVIDUAL REPRODUCTION IN THE REGULATION OF POPULATION ABUNDANCE

For the assessment of the role of a diversified reproduction of natural *E. verna* aggregations in the many-years' variations in total abundance, a model has been worked out of many-years' dynamics of a hypothetical population made up of individuals with an identical reproductive efficiency in every place within the biochore.

The point of departure for the working out of this model was the assumption of a uniform population density throughout the population area (thus with the same intensity of inter-individual interactions) and of constant biochore boundaries in the period analysed. Two extreme situations have been taken into account: (1) with a very low density of the initial population, equal to 2 seedlings per 0.01 m², and (2) with a very high density of the initial population, amounting to 55 seedlings per 0.01 m². To simplify the computation, in both cases the initial population consisted of 1000 seedlings; theoretically, they inhabited — respectively — 5 m² and 0.18 m² of surface area.

In the computation of the rate of survival of the seedling population until the fruiting and seed dissemination phases the mortality indices obtained in earlier field investigations (Symonides 1983a), appropriate to the particular density, were used. On the basis of the established number of adults in the given year, and the average natality indices obtained empirically for the density classes taken into account (Table II) the number of seedlings expected to emerge next year has been estimated, that is, the abundance of the initial population of the next generation. Calculations of this kind have been made for seven consecutive years.

The results of the simulation seem to be fairly interesting. As expected — in the case of both a low and a high density at the initial stage there occur rhythmic variations in population abundance between successive years (Fig. 8). The frequency and amplitude of the oscillations in the two situations considered are very similar, whereas the direction of the yearly changes, and the absolute value of abundance attained in years of a low and a high level are very different.

At a low initial density there is an over 30-fold increase in population abundance in the following year, whereafter the abundance returns to the initial level and then grows again rapidly. A reversed course of changes is observed in the situation where there is a high density in the initial population: in the first year the level of abundance drops considerably then rises to the original value, whereafter it falls again. Every other year, irrespectively of the density at the beginning, the population abundance is similar to the initial abundance (Fig. 8).

Thus if the reproduction of different individuals is identical, then, regardless of whether its efficiency is high or low, a population is subject to big, regular changes over a many-years' cycle. The value of the natality index determines the absolute population abundance, both in the years in which it is high and in those in which it is low.

With a diversified individual reproduction, associated with a diverse spatial structure in the biochore, the population as a whole is characterized by a high

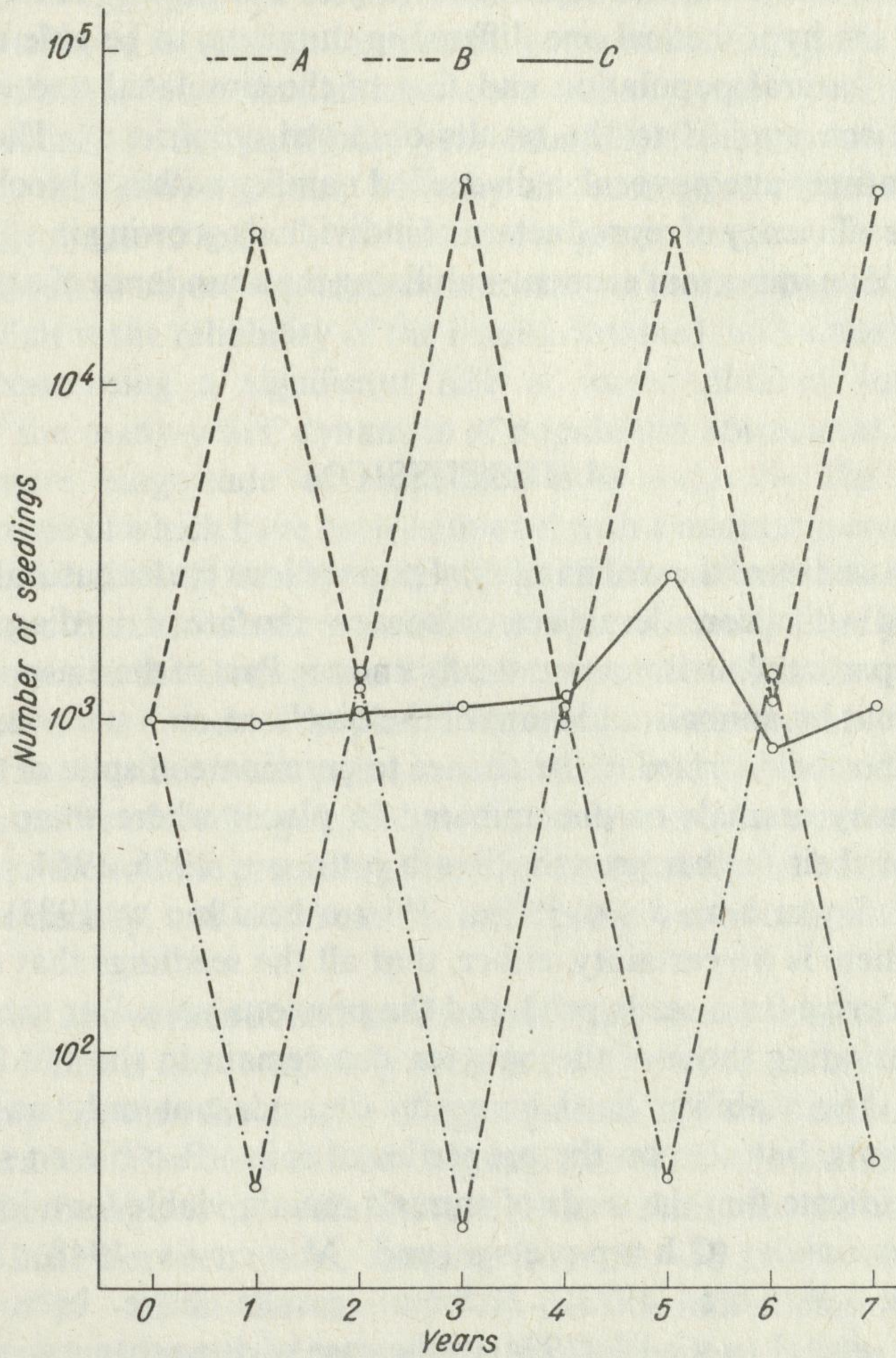


Fig. 8. Changes in number of seedlings over a many-years' cycle in the case of a low (A), high (B) and diversified (C) density of a population with initial number of 1000 individuals
 A and B — hypothetical populations with a uniform spatial structure and an initial density of — respectively — 2 and 55 seedlings per 0.01 m^2 , C — natural population; data acc. to Symonides (1983a)

equilibrium of numbers over a many-years' cycle. The number of seedlings emerging varies slightly from year to year, and if there occur wider variations due to weather anomalies, a quick return to the initial level is observed. The curve which represents the situation in question in Figure 8 has been worked out according to data from earlier studies carried out under natural conditions (Symonides 1983a). As the initial population and the hypothetical one differed in numbers, to be able to compare the dynamics of the natural population and that of the simulated one, an appropriate correction has been applied to the results obtained empirically. The result of this comparison is entirely unequivocal: a diversified natality within a biochore, caused by differences in the efficiency of reproduction of individuals growing in aggregations that differ in density, is an important element stabilizing the abundance of a population over a many-years' cycle.

4. DISCUSSION

Results from studies of the real natality of populations under natural conditions are usually burdened with a considerable error, because the fate of the diaspores after their freeing from the parent plant is not practically known. Part of the diaspores may get out (e.g., be carried out by animals and man) of the biochore, sink with water into deeper soil layers and thus be deprived of the chance to germinate in spite of their remaining viable, be eaten by animals or disseminated in places where there are conditions unfavourable for their further growth (Rabotnov 1956, 1964, Major and Pyott 1966, Symonides 1978a, Pirožnikov 1983).

In general, there is no certainty, either, that all the seedlings that emerged in the particular year derive from seeds produced the previous year. For the seeds of many plant species, including those of therophytes, can remain in the soil for many years without losing their viability. Seed longevity depends not only on the biological properties of plants, but also on the properties of soils (Roberts 1970, 1972).

Some data indicate that the seeds of annuals remain viable for a longer time than the seeds of perennials (Chapness and Morris 1948, Major and Pyott 1966, Went 1973). Different results have been obtained by Pemadasa and Lovell (1974) in the case of dune therophytes, the seeds of which can germinate only for one growing season and lose their viability thereafter. The life strategy of the seeds can thus be different from the strategy of the plants that produce them (Harper and White 1971).

From the above considerations follows that it is as a rule rather difficult to demonstrate a causal relationship between density and the fecundity of adult individuals of a population, and the number of seedlings in the next generation. Because of this, among other things, the studies presented in this paper have been restricted to an analysis of natality only in the case of a very low and a very high density, so that the effects of possible inter-individual interactions could be sufficiently evident. For the same reason also, the different plots were chosen not only on account of a

similar number of seedlings, but also on account of their location in the phytocoenosis, whereas the field studies have been supplemented with an analysis of the germination capacity of seeds, and of their longevity under laboratory conditions.

The studies have shown that, depending on the density at the seedling stage, different *E. verna* aggregations are characterized by a varying natality index, while the diversified natality is in turn an important factor maintaining the abundance of the seedling populations at a similar level over a many-years' cycle. Spatial relations among individuals in the particular year thus affect the size and structure of the population in the following year, whereby the ecological effects of inter-individual interactions continue to exist in the successive generations.

As it is difficult to objectively assess the natality of natural populations, the question arises as to what is the reliability of the results obtained, and whether they justify the conclusion concerning a significant role of inter-individual interactions in the regulation of the many-years' dynamics of population abundance.

The ultimate magnitude of reproduction is naturally the result of several parameters, some of which have been estimated with a minimum error at the most (the number of seeds in the soil, number of seedlings, number of individuals surviving till the fruiting phase), others have been assessed only approximately (seed production). There may be objections to the assumption that all the seeds found in the surface soil layer of the different plots were seeds of the plants that had grown in those plots in the preceding growing season. Another weak point in the studies was the fact that the relationship between the number of seedlings in the particular year and the number of seeds that had penetrated into the soil the preceding year was analysed on the basis of data from plots with the same density, and not from the same plots, but of course there was no other possibility.

Though the above-mentioned methodical draw-backs lead to an assessment of reproduction which is not completely accurate, they do not distort the basic picture of the relationship between the density of aggregations and the number of individuals in the next generation. For there can be only small errors in the assessment of particular parameters, this being due to several factors: (1) as a character, the number of seeds in a silicle varies little between years, ranging from 50–53 in the case of low-density individuals, to 19–22 in the case of high-density individuals (Symonides 1983b); the value of seed production in plots, determined on the basis of an exact number of fruiting individuals and silicles, as well as an average number of seeds in a silicle is loaded with a slight error; (2) on account of the location of the plots in the vicinity of large grass tussocks, and the fairly large distances between plots, as well as the small size of *E. verna* individuals and lack of any adaptations for distribution by wind on their seeds, it may be assumed with a high probability that the seeds really are shed around the parent plants; (3) the very small number of seeds remaining in the surface soil layer after the germination phase, along with the finding that seeds are capable of germinating only in the case of shallow sowing suggest that the greater majority of, if not all, seedlings derive from seeds produced by plants of the preceding generation.

The very low natality index found for aggregations with a high initial density results from both the plastic reactions of individuals to the overcrowding stress and the short life history of *E. verna*. The conditions under which plants develop at their early life stages have a decisive effect on the rate of their phenological development, size and fecundity (Symonides 1983a, 1983b). Hence, though in highly compact aggregations a large number of seedlings and early-juvenile individuals die, the remainder of the plants that survive either do not attain the generative phase or are characterized by a very low fecundity. Therefore in plots with a high initial density the total seed production is considerably lower than in low-density plots.

A similar reaction to overcrowding has been found in many plant species, both annuals and perennials (Hodgson and Blackmann 1957, Puckridge and Donald 1967, Snell 1976, Symonides 1979a, 1979b, 1979c, Begon and Mortimer 1982). The magnitude of seed production, in general very high in plots of both density classes, is not the cause of the subtle differences in natality among aggregations of similar abundance. As has been revealed by studies, depending on the initial population density — a smaller or larger fraction of all seeds produced get into the soil. This seemingly unaccountable causal relationship between the two parameters is clarified by the results obtained from an analysis of the correlation: between the size of the surface area not overgrown in each plot, and the number of seeds in the soil.

In the seed dissemination phase plots with a high initial density — in spite of a high death rate in the earlier phases — are overgrown by five times as many individuals as are low-density plots. In the former case the leaf rosettes adhering to the ground cover a larger proportion of the surface potentially accessible to the falling seeds than in the latter case. It is worth noting that on account of the mechanism by which adult individuals exert influence on the number of seeds getting into the soil, fruiting individuals and infertile individuals play a similar role; in high-density plots infertile plants thus have an indirect effect also on the final natality index.

Only a small percentage of the total number of seeds present in the surface soil layer germinate. In this respect *E. verna* does not basically differ from many other plant species, both annuals and perennials (Kropáč 1966, Naylor 1972a, 1972b, Symonides 1974a, 1979d, Harper 1977). Noteworthy is the fact that at a higher seed density in the soil larger proportion of seeds germinate, and, depending on the density, this fraction can be on an average three times higher than at a low seed density. Whitlow-grass seeds probably secrete some germination-stimulating substances which act upon adjacent seeds. A more efficient germination-stimulating effect of such secretions on seeds in aggregations than on those in dispersal would therefore be justifiable (Linhart and Pickett 1973, Symonides 1979d). This view seems to be supported by the result of an analysis of the seed germination capacity in laboratory systems with a uniform, relatively thin, sowing rate: differences in seed germination capacity, depending on the density of the parent plants, were much smaller.

The higher percentage, observed each year, of germination of seeds produced by plants growing in dispersal than of those growing in compact aggregations, irrespective of the experimental conditions, may be related to the significantly higher weight of the seeds, that is, a higher storage of materials (Black 1956, Twamley 1967, Symonides 1978b).

Unfortunately, under natural conditions it is hard to establish the fate of the seeds which had got into the soil, but did not germinate in the following growing season. Studies of seed longevity in laboratory systems indicate that for several years a small proportion of seeds may germinate each year, provided the soil layer covering them is not too thick. In plots the number of such seeds in the soil was small. They probably became the spoils of animals, were washed into the soil with sinking rainwater, or translocated outside the plots. However, significant for the interpretation of the results is not a precise analysis of the fate of the diaspores, but the fact that the germinating fraction varies insignificantly between plots of the density classes compared, and varies relatively little from year to year. It may, therefore, be concluded that subject to an insignificant variation is also the role of extra-population factors in the regulation of the relationship between the number of seeds in the soil and the number of seeds that germinate in the next growing season.

To sum up, the studies have demonstrated that spatial relations among individuals to a large extent determine their physiological condition, growth and development rates, fecundity, reproductive potential, and thereby — mortality and natality rates. By influencing these processes they also affect the seasonal and many-years' abundance dynamics (cf. Andrzejewski and Symonides 1982). A comparison of the dynamics of a natural population, thus a population with a diversified spatial structure within the biochore, with that of a simulated population — with the assumption of constant distances between individuals — clearly indicates a causal relationship between the diverse natality of the different aggregations in the space occupied by the population and the constant population abundance in time, over a many-years' cycle.

The discussion of the results does not include the effect of weather conditions on the value of the particular parameters which in consequence regulate the value of the natality index. Varying in the particular years was primarily the production of seeds, rather strongly dependent on the amount of precipitation during the growth and development of therophytes (Newman 1965, Symonides 1979a, 1983b); to a lesser extent also the size of leaf rosettes, which combined together resulted in a relationship, different in the particular years although not linear, between the number of seeds in the soil and their production (cf. Pirożnikow 1983). Apart from this, an analysis of the capacity and speed of seed germination in laboratory systems indicates that under natural conditions the moisture and the chemical properties of the substrate can modify the germination. Since the problems related to the effect of external factors on the magnitude of reproduction of a population were not directly connected with the basic aim of the present studies, the effect of the environment on the

many-years' abundance dynamics of *E. verna* populations has not been discussed in more detail.

5. SUMMING-UP CONCLUSIONS

1. Both seasonal and many-years' abundance dynamics of an *E. verna* population is closely related to its spatial structure, the number of aggregations and their density.
2. The dynamics of spatially separated aggregations varies seasonally over a many-years' cycle, depending on the number of individuals and distances among them.
3. The intensity of inter-individual interactions increases with the growing density of the aggregations. This is manifested by: (a) increased mortality, (b) limited individual size and fecundity, (c) decreased natality.
4. Differences in the density of the particular aggregations in the area of an *E. verna* biochore are the basis factor maintaining an equilibrium of size of the population as a whole over many-years' cycles.
5. A close, negative correlation between the densities of aggregations in the same places of a biochore from year to year is the result of an ecological continuity of the effects of inter-individual interactions from generation to generation.
6. Factors that are external to the population may cause changes in the absolute number of individuals, but they do not alter the system of relationships and inter-individual interactions.

6. SUMMARY

The present paper completes a wide-scope series of studies concerned with an analysis of the role of inter-individual interactions in the regulation of seasonal and many-years' abundance dynamics of *E. verna* populations. Two earlier publications dealt with the effect of intra-population interactions on the survival, growth rate, development rate, and individual size and fecundity (Symonides 1983a, 1983b). The aim of the studies presented in this paper was to clarify both the cause and effects of regular, yearly variations in the number of seedlings in different parts of the population area. The scope of the research included an assessment of the natality of spatially separated aggregations of individuals with different initial density, an analysis of factors responsible for the value of the natality index, and an assessment of the role of differences in the natality of the particular aggregations in the regulation of the many-years' population abundance dynamics.

Field investigations were carried out in the years 1973–1976 in a patch of Festuco-Koelerietum glaucae. Near permanent areas in which the survival and development of *E. verna* were analysed, two series of plots, each of 130 plots 0.01 m² in size, were laid out, with seedling densities 1–4 and 50–60. Each year counts were made of adult individuals, seeds produced, seeds that got into the soil and seedlings which developed in the following growing season, and the leaf rosettes of adult plants were measured to establish the coverage of the soil surface. The number of seeds remaining in the soil on the termination of the germination phase was determined once during the study period.

In the laboratory, the germination capacity and the speed of germination were checked of the seeds of individuals that grew under low and high density conditions, and the weight and longevity of seeds were determined. A hypothetical population dynamics model has been worked out with uniform density

throughout the area: very low or very high, using empirically determined mortality and reproduction indices for aggregations with different initial densities.

The studies have shown that the numbers of seedlings and adult individuals in the plots of the density classes compared changed regularly from year to year (Fig. 1). A close, negative correlation has been found between the number of seedlings and the number of adult individuals in the particular plots in a given year, and the number of seedlings developed in the same plots the following year (Figs. 2, 3); a positive correlation has been found between the number of seeds in the soil and the density of seedlings having developed the following year (Fig. 4). Calculated per unit area, seed production is several times higher in low-density plots than in high-density plots, and it differs between years (Table I). The number and proportion of seeds getting into the soil, thereby the density of seedlings in the next growing season, depend on the degree of soil-surface coverage by the leaf rosettes of the whitlow-grass (Table II, Fig. 5 a, b).

Seed germination capacity is many times lower under natural conditions than in the laboratory (Tables II, III). It has been found that seeds of plants derived from highly crowded aggregations are lighter and have lower germination capacity than seeds of plants free of neighbours' pressure (Fig. 7). However, greater differences in this respect occur under natural conditions. Plant density has no significant effect on the longevity of the seeds (Fig. 8). Theoretically, *E. verna* seeds are capable of germination for several years after their harvest, but in the soil of the different plots few seeds were found capable of germination on the termination of this phase.

The ultimate result of the natality of the particular aggregations is determined by the following: number and fecundity of survivors, number of seeds in the surface soil layer and their germination capacity. All these parameters are negatively correlated with the density of the aggregations at the seedling stage. For this reason, the natality of aggregations with a low initial density is on an average 161 times higher than that of the aggregations with a high density in the seedling phase (Table II).

The hypothetical population dynamics model, in which a uniform initial density is assumed, points to the occurrence of regular, very wide oscillations in numbers over a many-years' cycle (Fig. 8). The studies have thus proved that spatially diversified natality and mortality have a significant effect on the maintenance of a balanced many-years' population abundance dynamics.

Under natural conditions the germination capacity of *E. verna* seeds is low, as in that of many other plant species (K r o p a č 1966, N a y l o r 1972a, 1972b, S y m o n i d e s 1978b, 1979a, 1979b, 1979c). Similarly to other species, a close relationship has also been found between density and death risk, and individual reproduction magnitude and reproductive success (H a r p e r 1977, B e g o n and M o r t i m e r 1982).

To sum up, the present series of studies have demonstrated that spatial relations among individuals to a large extent determine their physiological condition, and thereby — the mortality rate of the population. By exerting an influence on these processes they also affect the seasonal and many-years' abundance dynamics (cf. A n d r z e j e w s k i and S y m o n i d e s 1982). Differences in density among the aggregations in the area of an *E. verna* population biochore are thus the basic mechanism responsible for the maintenance of a state of abundance equilibrium of the population in a many-years' cycle, or a quick return to this state after disturbances caused by weather or phytocoenotic abnormalities (cf. S y m o n i d e s 1983a and Fig. 8).

7. POLISH SUMMARY

Praca jest ostatnią częścią szerszych studiów, poświęconych analizie roli oddziaływań między osobnikami w kształtowaniu sezonowej i wieloletniej dynamiki liczebności populacji *E. verna*. W dwóch wcześniejszych publikacjach omówiono wpływ interakcji wewnątrzpopulacyjnych na przeżywanie, tempo wzrostu, tempo rozwoju, wielkość i płodność osobników (S y m o n i d e s 1983a, 1983b). Celem badań zaprezentowanych w niniejszej pracy było wyjaśnienie zarówno przyczyn, jak też skutków corocznych, regularnych zmian liczebności siewek w różnych miejscach areału populacji. Zakres badań obejmował ocenę rozrodczości przestrzennie odgraniczonych skupisk osobników o różnym zagęszczeniu początkowym,

analizę czynników oddziałujących na wielkość wskaźnika rozrodczości oraz ocenę roli zróżnicowanej rozrodczości poszczególnych skupisk w kształtowaniu wieloletniej dynamiki liczebności populacji.

Badania terenowe prowadzono w latach 1973–1976 w płacie *Festuco-Koelerietum glaucae*. W sąsiedztwie stałych powierzchni, na których analizowano przeżywanie i rozwój *E. verna*, wyznaczono po 130 poletek o powierzchni 0,01 m², o zagęszczeniu siewek 1–4 i 50–60. Co roku liczono dorosłe osobniki, wyprodukowane nasiona, nasiona przedostające się do gleby, siewki w następnym sezonie wegetacyjnym oraz mierzono rozetki dorosłych osobników dla ustalenia pokrycia powierzchni. Jednorazowo ustalono liczbę nasion pozostałych w glebie po fenologicznej fazie kiełkowania.

W warunkach laboratoryjnych sprawdzono zdolność i szybkość kiełkowania nasion osobników wyrosłych w niskim i wysokim zagęszczeniu oraz ciężar i długowieczność nasion. Opracowano model dynamiki hipotetycznej populacji o jednakowym zagęszczeniu na całym obszarze: bardzo niskim lub bardzo wysokim, korzystając z ustalonych empirycznie wskaźników śmiertelności i rozrodczości dla skupisk o różnym zagęszczeniu początkowym.

Badania wykazały, że z roku na rok zachodzą regularne zmiany liczby siewek i dorosłych osobników na poletkach porównywanych klas zagęszczeń (rys. 1). Między liczbą siewek i liczbą osobników dorosłych na poszczególnych poletkach w danym roku a liczbą siewek wyrosłych na tych samych poletkach w roku następnym istnieje ścisła korelacja ujemna (rys. 2, 3); dodatkowo natomiast są skorelowane liczba nasion w glebie i zagęszczenie siewek w następnym roku (rys. 4). Produkcja nasion w przeliczeniu na jednostkę powierzchni jest kilkakrotnie wyższa na poletkach z niskim niż z wysokim zagęszczeniem i zmienna w różnych latach (tab. I). Liczba i frakcja nasion docierających do gleby, a tym samym zagęszczenie siewek w następnym sezonie wegetacyjnym, są uzależnione od stopnia pokrycia powierzchni rozetkami liściowymi wiosnowki (tab. II, rys. 5 a, b).

Zdolność kiełkowania nasion w warunkach naturalnych jest wielokrotnie niższa niż w warunkach laboratoryjnych (tab. II, III). Stwierdzono, że nasiona roślin pochodzących z silnie zagęszczonych skupisk są lżejsze i charakteryzują się niższą zdolnością kiełkowania niż nasiona roślin wolnych od presji sąsiadów (rys. 7). Różnice pod tym względem są jednak większe w warunkach naturalnych. Na długowieczność nasion zagęszczenie roślin nie wywiera istotnego wpływu (rys. 8). Teoretycznie, nasiona *E. verna* są zdolne do kiełkowania przez kilka lat po zbiorze, jednak w glebie poszczególnych poletek znaleziono tylko nieliczne nasiona potencjalnie zdolne do kiełkowania po zakończeniu tej fazy.

Na końcowy efekt rozrodczości poszczególnych skupisk składa się: liczba i płodność osobników przeżywających, liczba nasion w powierzchniowej warstwie gleby i ich zdolność kiełkowania. Wszystkie te parametry są ujemnie skorelowane z zagęszczeniem skupisk w fazie siewki. Stąd też, rozrodczość skupisk o niskim zagęszczeniu początkowym jest przeciętnie aż 161 razy wyższa niż skupisk o wysokim zagęszczeniu w fazie siewki (tab. II).

Model dynamiki hipotetycznej populacji o wyrównanym zagęszczeniu początkowym wskazuje na występowanie regularnych, bardzo dużych wahań liczebności w cyklu wieloletnim (rys. 8). Badania dowiodły zatem istotnego wpływu zróżnicowanej przestrzennie rozrodczości i śmiertelności w utrzymaniu zrównoważonej dynamiki wieloletniej populacji.

Zdolność kiełkowania nasion *E. verna* w warunkach naturalnych jest niska, podobnie jak u wielu innych gatunków roślin (K r o p a č 1966, N a y l o r 1972a, 1972b, S y m o n i d e s 1978b, 1979a, 1979b, 1979c). Podobnie jak u innych gatunków, stwierdzono także ścisłą zależność między zagęszczeniem a ryzykiem śmierci, wielkością i sukcesem reprodukcyjnym osobników (H a r p e r 1977, B e g o n i M o r t i m e r 1982).

Reasumując, badania zaprezentowanego cyklu prac wykazały, że stosunki przestrzenne między osobnikami w znacznej mierze określają ich stan fizjologiczny, a w konsekwencji – intensywność śmiertelności populacji. Poprzez wpływ na te procesy – oddziałują także na sezonową i wieloletnią dynamikę liczebności (por. A n d r z e j e w s k i i S y m o n i d e s 1982). Zróżnicowane zagęszczenie poszczególnych skupisk na obszarze biochory populacji *E. verna* jest więc podstawowym mechanizmem utrzymania się stanu liczebnej równowagi populacji w cyklu wieloletnim, lub szybkiego powrotu do tego stanu po zaburzeniach spowodowanych anomaliami pogodowymi lub fitocenotycznymi (por. S y m o n i d e s 1983a i rys. 8).

8. REFERENCES

1. Andrzejewski R., Symonides E. 1982 – Organizacja przestrzenna populacji roślin i zwierząt [Spatial structure of plant and animal populations] – Wiad. ekol. 25: 635 – 651.
2. Begon N., Mortimer M. 1982 – Population ecology. A unified study of animal and plants – Blackwell Scientific Publications, Oxford – London, 200 pp.
3. Black J. N. 1956 – The influence of seed size and depth of sowing on preemergence and early vegetative growth of subterranean clover (*Trifolium subterraneum* L.) – Aust. J. agric. Res. 14: 20 – 38.
4. Chapness S. S., Morris K. 1948 – The population of buried viable weed seeds in relation to contrasting pasture and soil types – J. Ecol. 36: 149 – 173.
5. Falencka M. 1983 – Struktura i dynamika populacji *Impatiens noli-tangere* L. w różnych warunkach ekologicznych [The structure and population dynamics of *Impatiens noli-tangere* in the different ecological conditions] – Ph.D. Thesis, Warsaw University, Warsaw, 109 pp.
6. Falińska K. 1979 – Modifications of plant populations in forest ecosystems and their ecotones – Pol. ecol. Stud. 5: 89 – 150.
7. Grubb P. J., Kelly D., Mitchley J. 1982 – The control of relative abundance in communities of herbaceous plants (In: The plant community as a working mechanism. Special publications series of the British Ecological Society, Number 1, Ed. E. I. Newman) – Blackwell Scientific Publications, Oxford – London – Edinburgh – Boston – Melbourne, 79 – 97.
8. Harper J. L. 1977 – Population biology of plants – Academic Press, London – New York – San Francisco, 896 pp.
9. Harper J. L., White J. 1971 – The dynamics of plant populations (In: Dynamics of populations. Proceedings of the Advances Study Institute on "Dynamics of number in populations" (Oosterbeck, the Netherlands, 7–8 September 1970), Eds. P. J. den Boer, G. R. Gradwell) – Centre for Agricultural Publishing and Documentation, Wageningen, 41 – 63.
10. Hodgson G. L., Blackmann G. E. 1957 – An analysis of the influence of plant density on the growth of *Vicia faba*. Part 2. The significance of competition for light in relation to plant development at different densities – J. exp. Bot. 8: 195 – 219.
11. Inouye R. S., Biers G. S., Brown J. H. 1980 – Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals – Ecology, 61: 1344 – 1351.
12. Kropač Z. 1966 – Estimation of weed seeds in arable soil – Pedobiologia, 6: 105 – 128.
13. Law R. 1981 – The dynamics of a colonizing population of *Poa annua* – Ecology, 62: 1267 – 1277.
14. Linhart Y. B., Pickett II R. A. 1973 – Physiological factors associated with density-dependent seed germination in *Boisduvalia glabella* (Onograceae) – Z. Pflanzenphysiol. 70: 367 – 370.
15. Major J., Pyott W. T. 1966 – Buried viable seeds in California bunchgrass sites and their bearing on the definition of a flora – Veget. Acta Geobot. 13: 253 – 282.
16. Naylor R. E. L. 1972a – Aspects of the population dynamics of the weed *Alopecurus myosuroides* Huds. in winter cereal crops – J. appl. Ecol. 9: 127 – 139.
17. Naylor R. E. L. 1972b – Biological Flora of British Isles. 129. *Alopecurus myosuroides* Huds. (*A. agrestis* L.) – J. Ecol. 60: 611 – 622.
18. Newman E. I. 1965 – Factors affecting the seed production of *Teesdalia nudicaulis*. II. Soil moisture in spring – J. Ecol. 53: 211 – 232.
19. Palmblad I. G. 1968 – Competition studies on experimental populations of weeds with emphasis on the regulation of population size – Ecology, 49: 26 – 34.
20. Pemadasa M. A., Lovell P. H. 1974 – Factors affecting the distribution of annuals in the dune systems at Aberffraw, Anglesey – J. Ecol. 62: 379 – 402.
21. Piżnikow E. 1983 – Seed bank in the soil of stabilized ecosystem of a deciduous forest (Tilio-Carpinetum) in the Białowieża National Park – Ekol. pol. 31: 145 – 172.
22. Puckridge D. W., Donald C. M. 1967 – Competition among wheat plants sown at a wide range of densities – Aust. J. agric. Res. 18: 193 – 211.

23. R a b o t n o v Г. A. 1956 — Nekotorye dannye o soderžanii semjan v počve lugovykh soobščestv (In: Akademiku V. N. Sukačevu k 75 letju so dnja roždenija. Ed. V. B. Sočava) — Akad. Nauk SSSR, Moskva — Leningrad, 481 — 499.
24. R a b o t n o v T. A. 1964 — Opredelenie čislennosti živych semjan i plodov v počve i na ego poverchnosti — Polev. Geobot. 3: 133 — 140.
25. R a y n a l D. J., B a z z a z F. A. 1975 — Interference of winter annuals with *Ambrosia artemisiifolia* in early successional fields — Ecology, 56: 35 — 49.
26. R o b e r t s E. H. 1972 — Dormancy: a factor affecting seed survival in the soil (In: Viability of seeds, Ed. E. H. Roberts) — Chapman and Hall, London, 321 — 359.
27. R o b e r t s H. A. 1970 — Viable weed seeds in cultivated soils — Rep. Natn. Veg. Res. Stn. (1969): 25 — 38.
28. S n e l l T. W. 1976 — Effects of density on seed size and biochemical composition — Am. Midl. Nat. 95: 499 — 507.
29. S y m o n i d e s E. 1974a — Population of *Spergula vernalis* Willd. on dunes in the Toruń — Basin — Ekol. pol. 22: 379 — 416.
30. S y m o n i d e s E. 1974b — Morphological variability of *Spergula vernalis* Willd. from different dune biotopes of the Toruń Basin — Ekol. pol. 22: 417 — 440.
31. S y m o n i d e s E. 1974c — Grupowe właściwości populacji roślin wyższych [Group properties of populations of higher plants] — Wiad. ekol. 20: 337 — 355.
32. S y m o n i d e s E. 1977 — Mortality of seedlings in natural psammophyte populations — Ekol. pol. 25: 635 — 651.
33. S y m o n i d e s E. 1978a — Number, distribution and specific composition of diaspores in the soils of the plant association *Spergulo-Corynephorum* — Ekol. pol. 26: 111 — 122.
34. S y m o n i d e s E. 1978b — Effect of seed size, density and depth of sowing on the germination and survival of psammophyte seedlings — Ekol. pol. 26: 123 — 139.
35. S y m o n i d e s E. 1979a — The structure and population dynamics of psammophytes on inland dunes. I. Populations of initial stages — Ekol. pol. 27: 3 — 37.
36. S y m o n i d e s E. 1979b — The structure and population dynamics of psammophytes on inland dunes. II. Loose-sod populations — Ekol. pol. 27: 191 — 234.
37. S y m o n i d e s E. 1979c — The structure and population dynamics of psammophytes on inland dunes. III. Populations of compact psammophyte communities — Ekol. pol. 27: 235 — 257.
38. S y m o n i d e s E. 1979d — The structure and population dynamics of psammophytes on inland dunes. IV. Population phenomena as a phytocenose forming factors (A summing-up discussion) — Ekol. pol. 27: 259 — 281.
39. S y m o n i d e s E. 1983a — 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. — Ekol. pol. 31: 839 — 881.
40. S y m o n i d e s E. 1983b — Population size regulation as a result of intra-population interactions. II. Effect of density on the growth rate, morphological diversity and fecundity of *Erophila verna* (L.) C. A. M. individuals — Ekol. pol. 31: 883 — 912.
41. T w a m l e y B. E. 1967 — Seed size and seedling vigour in birdsfoot trefoil — Can. J. Plant Sci. 47: 603 — 609.
42. W e n t F. W. 1973 — Competition among plants — Proc. Natn. Acad. Sci. U.S.A. 70: 585 — 590.
43. W i l k o Ń - M i c h a l s k a J. 1976 — Struktura i dynamika populacji *Salicornia patula* Duval-Jouve [Structure and dynamics of populations of *Salicornia patula* Duval-Jouve] — Uniwersytet Mikołaja Kopernika. Rozprawy, Toruń, 156 pp.