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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

ABSTRACT: The seasonal growth rate, morphological variability and fecundity of Erophila verna were analysed for seven years in plots differing in seedling density. The relative growth rate of individuals is independent of density, whereas the size of the vegetative organs and the fecundity of the plants are significantly correlated with the density of seedlings. With the same initial abundance of a population, seed production will thus depend on its spatial structure, that is, on the number of aggregations formed by a specific number of seedlings.

KEY WORDS: Sand dunes, Erophila verna, relative growth rate of individuals, density-dependent factors, morphological diversity of individuals, fecundity of individuals.

C o n t e n t s

1. INTRODUCTION

From the ecological point of view the question of morphological variability of plants belonging to the same population resolves itself into two basic problems: (1) looking for some non-genetic sources of variability, and (2) assessment of the role of this variability.

Responsible for the non-genetic variability of individuals are both quantifiable environmental factors and specific effects of the joint action of the genotype and the environment (R i e g e r, M i c h a e l i s and G r e e n 1974). A no less important role, as suggested by the population studies of the last twenty years, can be attributed to the interactions between individuals, especially under the conditions of population overcrowding relative to the richness of the biotope (H a r p e r 1977).

Plant population overcrowding is a common phenomenon in natural ecological systems. The process of dying does not usually eliminate the whole "surplus" of individuals, and being plastic and, by nature, unable to actively translocate themselves, plants react to the necessity of sharing the biotope resources which are too scarce by a reduced fecundity (P a l m b l a d 1968). Under the conditions of mutual pressure of individuals drawing on the same pool of resources only the strongest of them attain an exuberant growth and produce a large number of diaspores; most of them vegetate in a state of "underdevelopment" without any chance to reproduce (H a r p e r and W h i t e 1974). Studies carried out so far also indicate that differences between individuals increase considerably as the density of the population grows (O b e i d, M a c h i n and H a r p e r 1967).

The above facts concern primarily laboratory systems. In natural ecosystems differences between the individuals of a population are probably the result of a simultaneous combined action of genetic, biotope, biocoenotic and intra-population factors. The determination of the real contribution of inter-individual actions to the maintenance of these differences is therefore rather difficult, especially in view of the variable environmental conditions, a complex population structure and differences in population density within the biochore.

An evaluation of the role of intra-population interactions among the factors responsible for the variability of individuals is an important link in an appropriate assessment of the importance of these interactions in the regulation of population abundance. This follows from the fact that differences between individuals are closely related to the uneven sharing-out of the resources at the disposal of the population as a whole, the uneven sharing-out being essential to its stability (Ł o m n i c k i 1980).

In the present study a trial has been undertaken for analysing the effect of intra-population interactions on the growth rate, morphological differences and fecundity of the individuals of a natural population of Erophila verna. On account of the objective of the study, the growth rate, morphological characters, and fecundity of the individuals were investigated for several years in natural, spatially separated aggregations consisting of a varying number of individuals separated by different distances, thus being subject to intra-population interactions differing in intensity.

The choice of the study object was not fortuitous. An annual population of E. verna inhabits homogeneous, scantly overgrown sand areas, and completes the life history before the period of an intensive growth of the remaining species of the phytocoenosis (S y m o n i d e s 1983). So it is almost a model natural object for studying the intra-population interactions, consisting of even-aged individuals acting on each other in a similar way throughout the biochore, without any major disturbances from individuals of other plant species. In this situation it was possible to assume that: (1) the intensity of the interactions between the individuals of E. verna is first of all the function of the distances separating them, and (2) the intra-population relations may vary from year to year, because of different weather conditions during the growth and development of the individuals.

This paper represents part of wider studies carried out for the assessment of the effect of inter-individual interactions on the seasonal and many-years' population dynamics of E. verna. The first paper of the series contains a discussion of the course of seasonal changes in the number of individuals in relation to density, and an analysis of the rate of plant development under different pressure of individuals of the same species (S y m o n i d e s 1983). The third, the last, paper of the series (S y m o n i d e s - in press) will present the results of experimental investigations the aim of which was to determine the longevity of seeds, their ability to germinate, and the germinating conditions. The investigations were expected to show whether differences in the fecundity of individuals are a factor regulating the fecundity of the population, and whether fecundity is a mechanism regulating the abundance of an E. verna population, as important as mortality.

2. METHODS

The field studies were carried out in the years 1968-1974 in a patch of Festuco-Koelerietum glaucae Klika 1931, partially in the same four areas (each of 4 m^2) in which the survival and development of E. verna had been analysed (S y m o n i d e s 1983). Each area was divided into 400 plots, each of 0.01 m^2. Each year at the beginning of the growing season plots were selected to represent five density classes 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 plots of the particular classes were as follows: 10-12 cm, 2--4 cm, 1.0-1.5 cm, 0.4-0.8 cm and less than 0.2 cm, respectively. The seedlings growing in these plots represented 70.3% (in 1970) to 84.6% (in 1973) of the total number of individuals found within the study areas.

The analysis of the growth rate of individuals under different density conditions was based on 21 thousand measurements. Six times during each growing season: towards the end of the seedling phase, vegetative growth, budding, flowering, fruiting and seed disseminating a measurement was made of 500 randomly selected individuals representing the five density classes - 100 per class. If the number of density class I plots was less than 100, additional plots were laid out in the immediate vicinity of the area. For each density class separately the average value was calculated of the character studied, as well as the standard deviation and variability coefficient.

A more complete analysis of the morphological diversity of the individuals was always carried out only once a year, in the fruiting phase. The following characters were taken into account: stalk length (if a plant had more than one stalk, only the longest of them was measured), root length, diameter of the leaf-rosette, number of stalks, number of silicles. As it was necessary to dig up the plants, the material to be studied was collected outside the permanent areas, but always from plots of the same size and representing the same seedling density classes. For this purpose, in early spring each year 100 additional plots of density classes I and II were chosen, and 20 plots of each of the remaining classes. From each of these plots 100 individuals were taken at random for measurements.

To estimate the average number of seeds per a silicle, a sample of 100 silicles was randomly taken from the plants of each of the density classes. The product of the number of silicles and the average number of seeds per a silicle defines the value of individual seed production, being therefore an index of the fecundity of an individual. On the basis of the known number of plants representing the different density classes, and the known fecundity of these plants the contribution was determined of the individuals of each of the classes to the total seed production.

The statistical elaboration of the results consisted in the calculation of the mean values of the particular characters, confidence intervals and correlation coefficients for determining the correlation between characters.

The average, for the seven-year study period, value of the morphological characters of individuals growing in density classes II, III, IV and V were compared with the average values of the same characters in individuals representing class I, by using the Jentys-Szaferowa (1959) method.

The relationship between the density of seedlings and the fecundity of individuals growing under different density conditions was assessed on the basis of the values of the coefficient of correlation and the coefficient of regression. Taken into account in the calculations was a seven-year average fecundity of individuals growing in plots differing in respect of density exactly by 5 seedlings in the interval of 1 to 56. Each year each density variant was represented by 10 replications.

In all calculations the level of significance of 0.05 was adopted.

Data on the floristic composition in the study areas and weather conditions during the growth and development of E. verna are presented in the first paper of the present series (S y m o n i d e s 1983).

3. RESULTS

3.1. Course of the growth of individuals under different density conditions

The results from measurements of E. verna individuals in the particular phenological phases indicate several regularities. Regardless of weather conditions, seed germination dates and density, the size of the seedlings was almost identical each year, ranging from 0.27 to 0.29 cm. The seedling phase is the only period when there are not virtually any differences between the individuals of a population. In the next phase, in as short a time as several days very clear differences can already be seen which persist till the end of the life history of the whitlow grass (Fig. 1).

Another regularity is the relationship, recurring every year, between the density of seedlings and the height they attain in the next life stages. From the vegetative growth phase on the greater the distances separating the seedlings, the taller were the plants, relatively small differences being found only between class IV and class V individuals.

It should be noted that striking density differences between plots of the particular density classes occur only at the early life stages of the population. Later on, as a result of a much

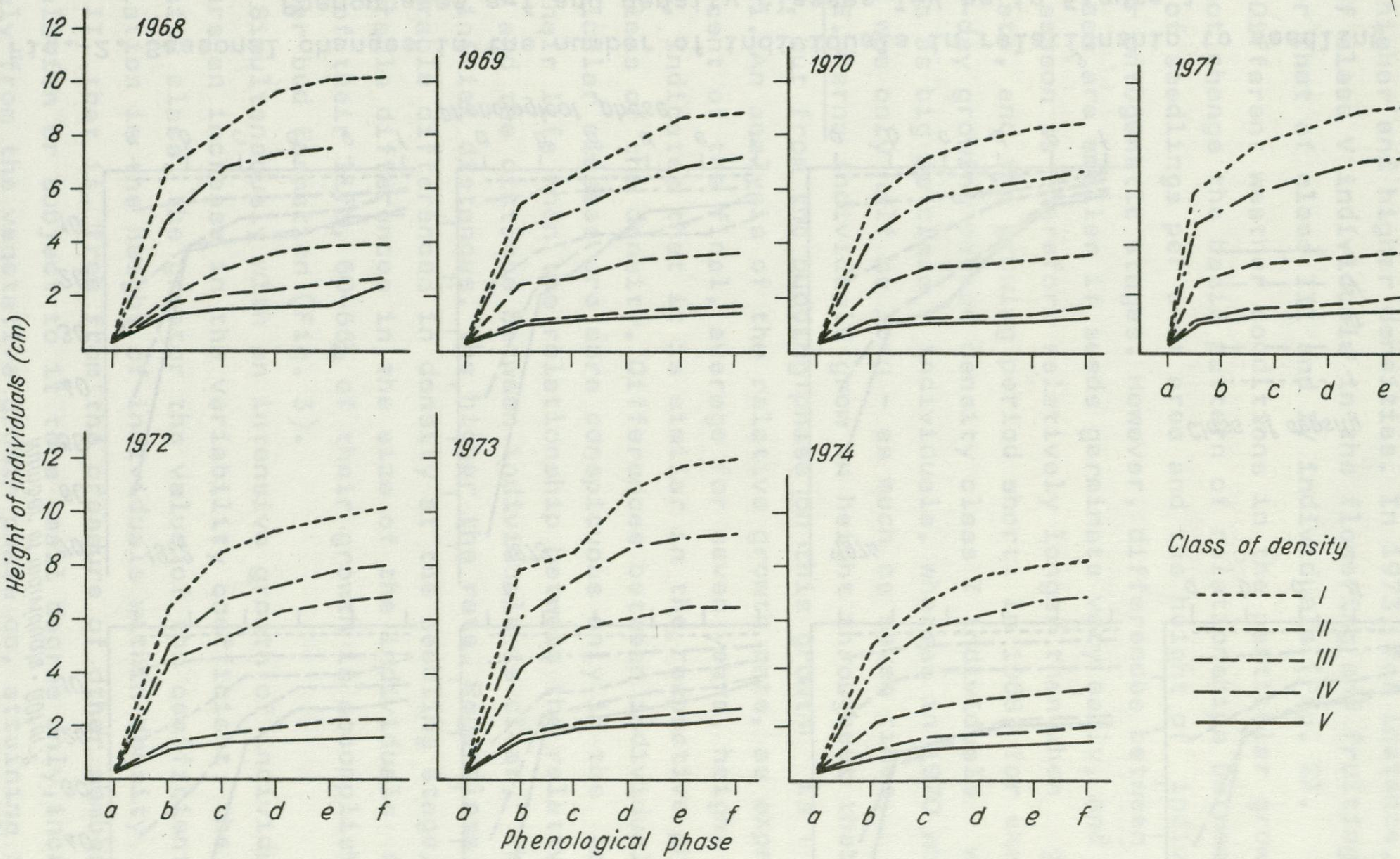

Fig. 1. Course of seasonal growth of individuals in relationship to seedling density

Phenophases: a - seedling, b - vegetative growth, c - budding, d - flowering, e - fruiting, f - seed-dissemination. Density classes according to the number of seedlings grown in an area of 0.01 m^2: I - 1-2, II - 5-10, III - 15-30, IV - 35-50, V - $\geqslant$55

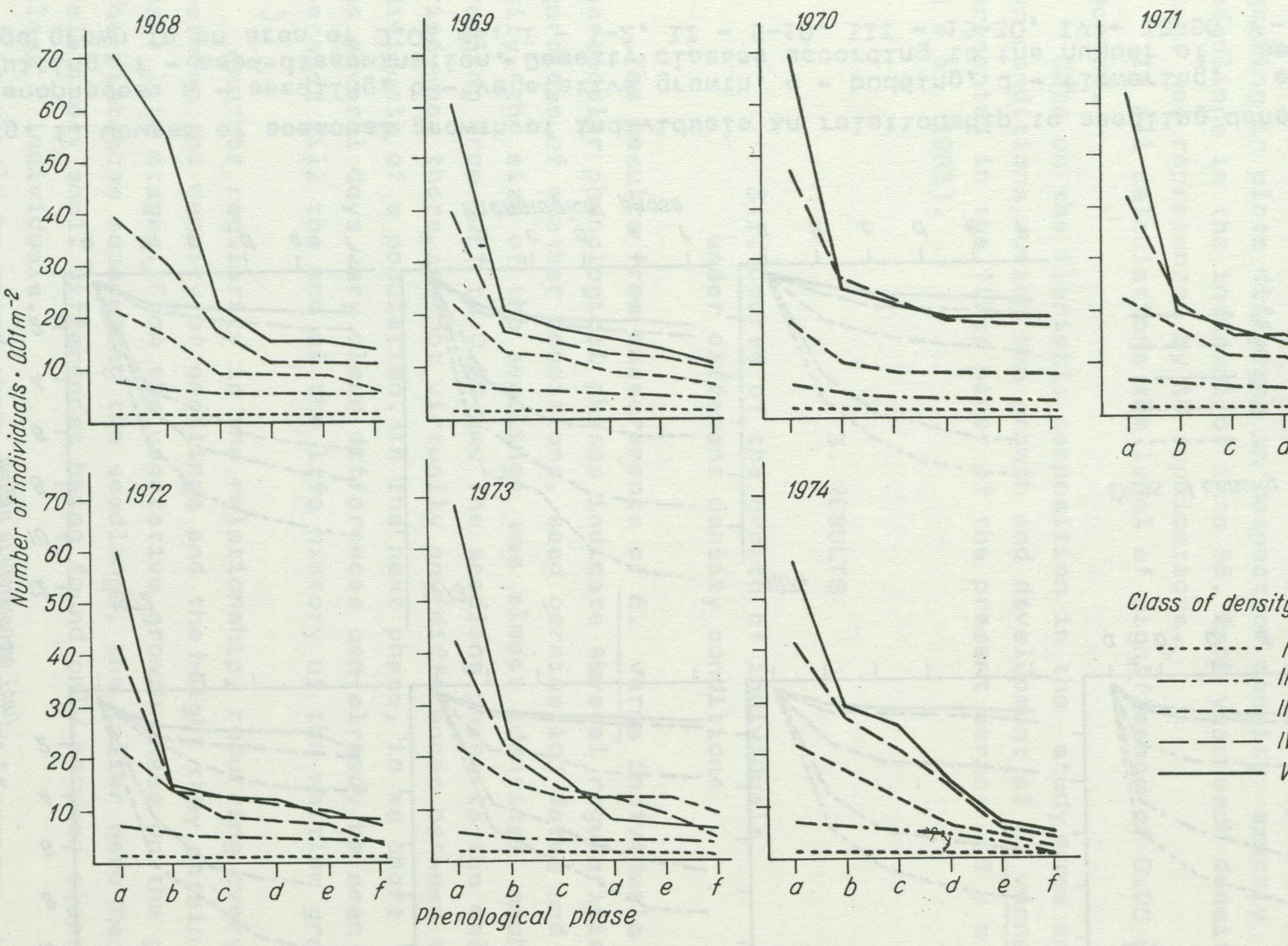

Fig. 2. Seasonal changes in the number of individuals in relationship to seedling density

Phenophases a-f and density classes I-V as in Figure 1 higher death rate in class IV and V plots than in those of the remainder of classes they become several times smaller. In some years there simply occurs a reversed sequence of plots representing higher and higher densities. In 1973, for instance, the density of class V individuals in the flowering and fruiting phases was lower that of class III and IV individuals (Fig. 2).

Different weather conditions in the particular growing seasons do not change the basic pattern of relationships between the number of seedlings per unit area and the height of individuals in later ontogenetic stages. However, differences between the density classes are smaller if seeds germinate very early, and the growing season is therefore relatively longer than when germination is late, and the growing period short. In 1968, for example, with a 64-day growing period density class I individuals were four times as big as class V individuals, whereas in 1970 when the period was only half as long - as much as seven times.

E. verna individuals grow in height throughout their life history, but from the budding phase on this growth is relatively small. An analysis of the relative growth rate, as expressed in per cent of the final, average for seven years, height of individuals, indicates that it is similar in the respective phases, regardless of the density. Differences between individuals of the particular classes are more conspicuous only in the last period of their life when the relationship between the relative growth rate and the distance between individuals is clear, the shorter the initial distances, the higher the rate. Regardless of the considerable differences in density at the seedling stage, and considerable differences in the size of the individuals towards the end of their life, 60-66% of their growth is accomplished before flower bud formation (Fig. 3).

Simultaneously with an intensive growth of individuals there occurs an increase in the variability coefficient; the higher the density class, the greater the value of the coefficient (Fig. 4). Variation in the height of individuals within density classes I and II, that is, free from the pressure of other members of the population or subject to it to a small degree only,increases very slowly from the vegetative growth phase on, attaining the highest value in the fruiting period whereafter it falls gradually.

The same direction of changes in the value of the coefficient

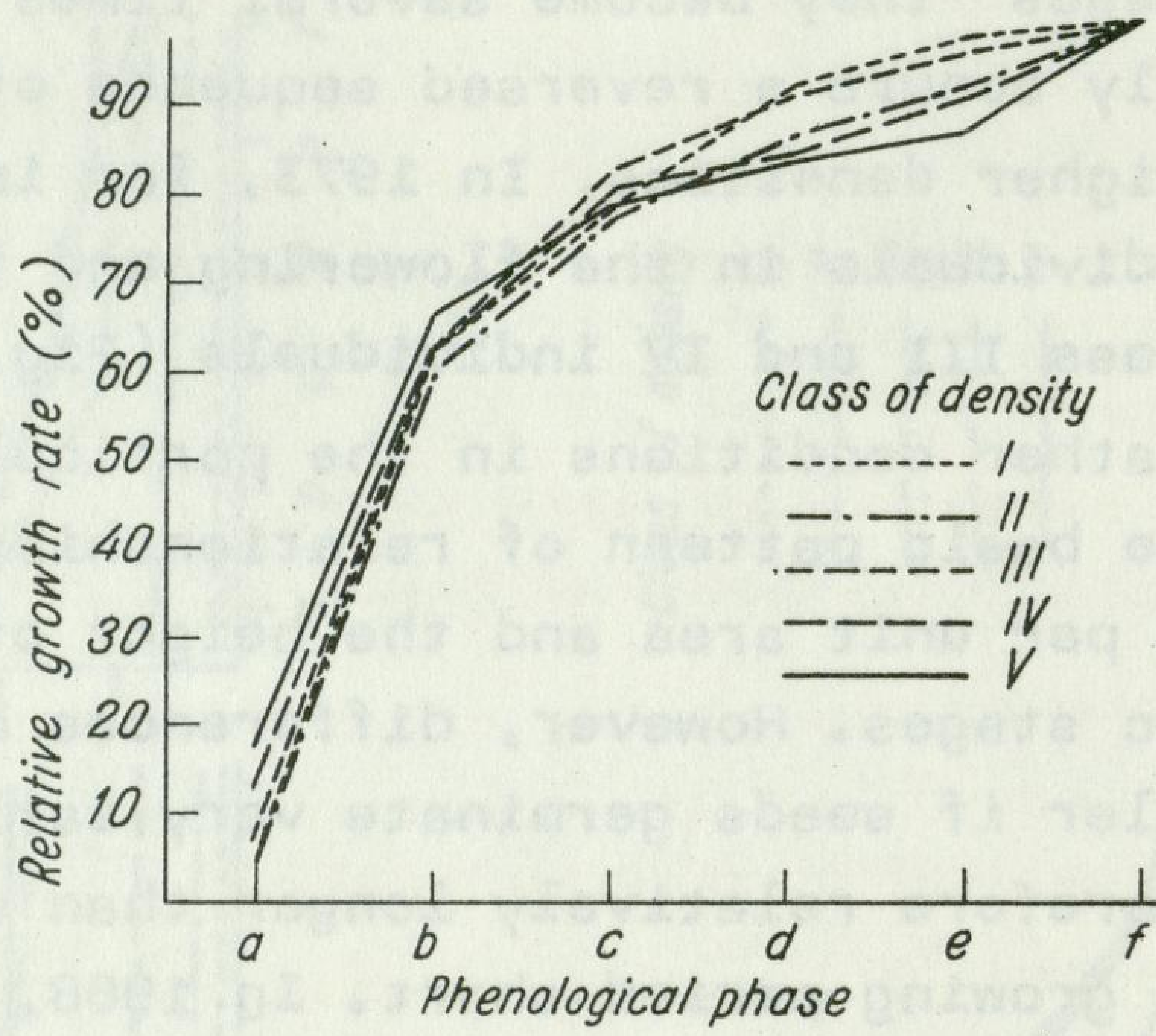

Fig. 3. Relative growth rate of individuals representing different seedling density classes (average values for seven years)

Phenophases a-f and density classes I-V as in Figure 1

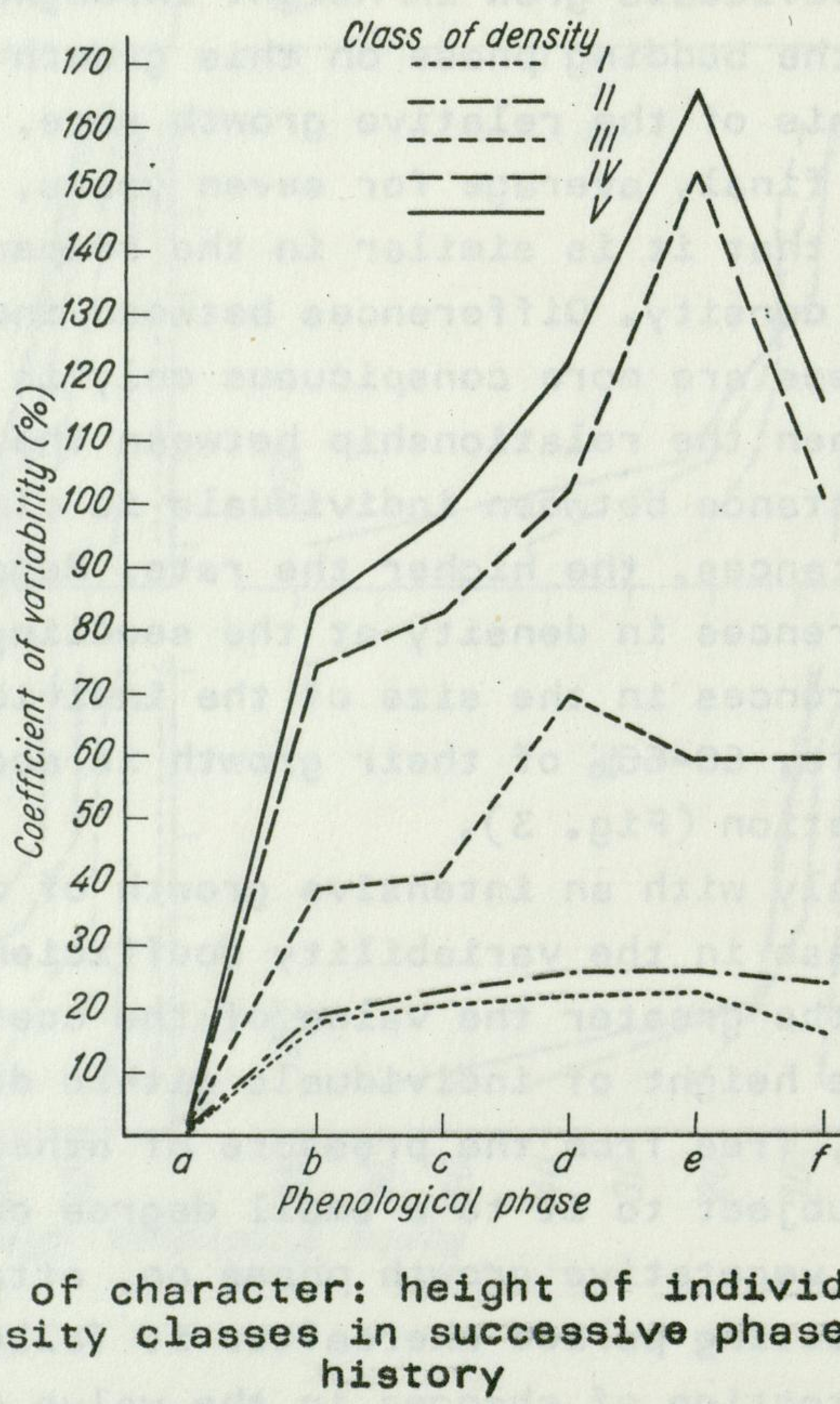

Fig. 4. Variation of character: height of individuals representing different density classes in successive phases of their life history

Phenophases a-f and density classes I-V as in Figure 1 has been found for plots of classes IV and V, but in this case the growth and decrease of its value were rapid. The variability of the character studied was in each phase greater than at a low density. The value of the coefficient changed stepwise in the intermediate density class, where it attained the maximum still in the flowering phase (Fig. 4).

3.2. Effect of density on the morphological features of individuals

All the morphological characters of fruiting E. verna individuals taken into account in the biometric analysis can be included among plastic characters. This is indicated on the one hand by conspicuous differences between individuals of the same density class in the consecutive growing seasons, and on the other hand by differences, recurring every year, between individuals depending on the density under which they grew. In the latter case the confidence limits calculated for mean values of the particular characters overlap only partially when class IV and V individuals are compared (Fig. 5). Such a result shows that the value of each character is affected by the influence of two groups of factors: weather conditions and intra-population interactions.

Each year each character attains a higher value if the density of individuals in the seedling phase is lower, the lower the density, the higher the value of the character. The different weather conditions in the particular years, and particularly the duration of the life history, determine only the absolute differences between the values of the respective characters. Individuals of the low density classes were to a larger extent subject to the action of external factors than were those of the high density classes. Hence under favourable external conditions and with a long life history of the population (1973 and 1968) differences between the respective characters of individuals representing extreme density classes are considerably greater than in years with an unfavourable system of climatic factors or delayed germination (1969 and 1974).

The comparison of the average, for the study period, values of characters in the particular density classes, made by using J e n t y s - S z a f e r o w a ' s (1959) method, makes possible an unequivocal evaluation of the effect of the interactions between individuals on their habitus and size. The unit of reference adopt-

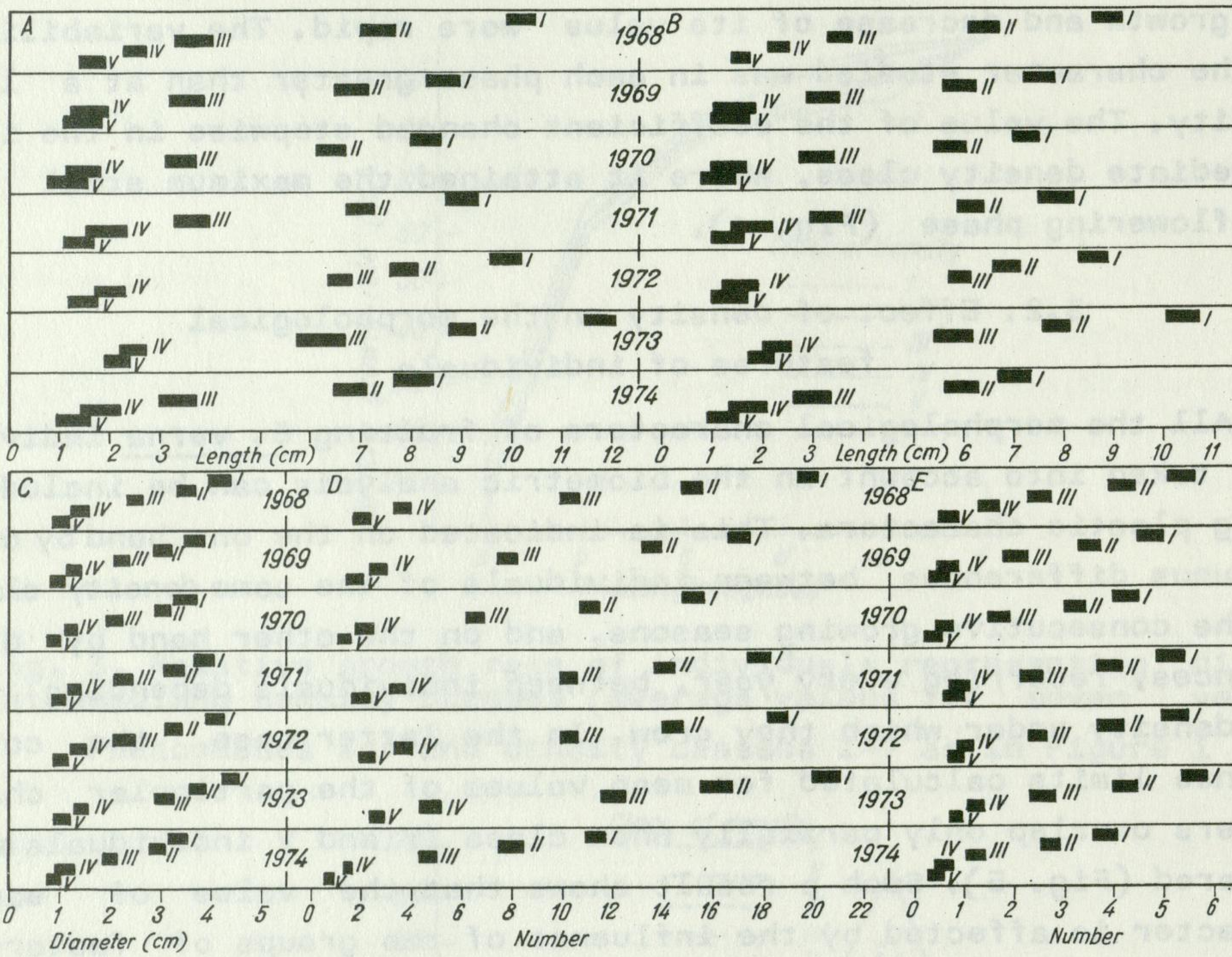

Fig. 5. Confidence intervals for average value of the morphological characters of individuals representing different density classes

A - stalk length (plant height), B - root length, C - leaf-rosette diameter, D - number of silicles, E - number of stalks. Density classes I-V as in Figure 1

ed in this analysis was the characters of individuals representing class I, that is, free from the pressure of neighbours (Fig. 6).

The course of the curves indicates that E. verna individuals react strongly to the presence of other members of the population in their immediate vicinity. Compared with the unit of reference, individuals grown under higher-density conditions show a shorter stalk and root, smaller leaf-rosette, smaller number of stalks and smaller number of silicles.

The great similarity of class IV and V individuals suggests that above a certain threshold of numbers, amounting to about 55 seedlings per 0.01 m^2, any further increase in density has a weaker and weaker effect on the morphological features of individuals.

The shape of the curves in Figure 6 indicates a similar degree

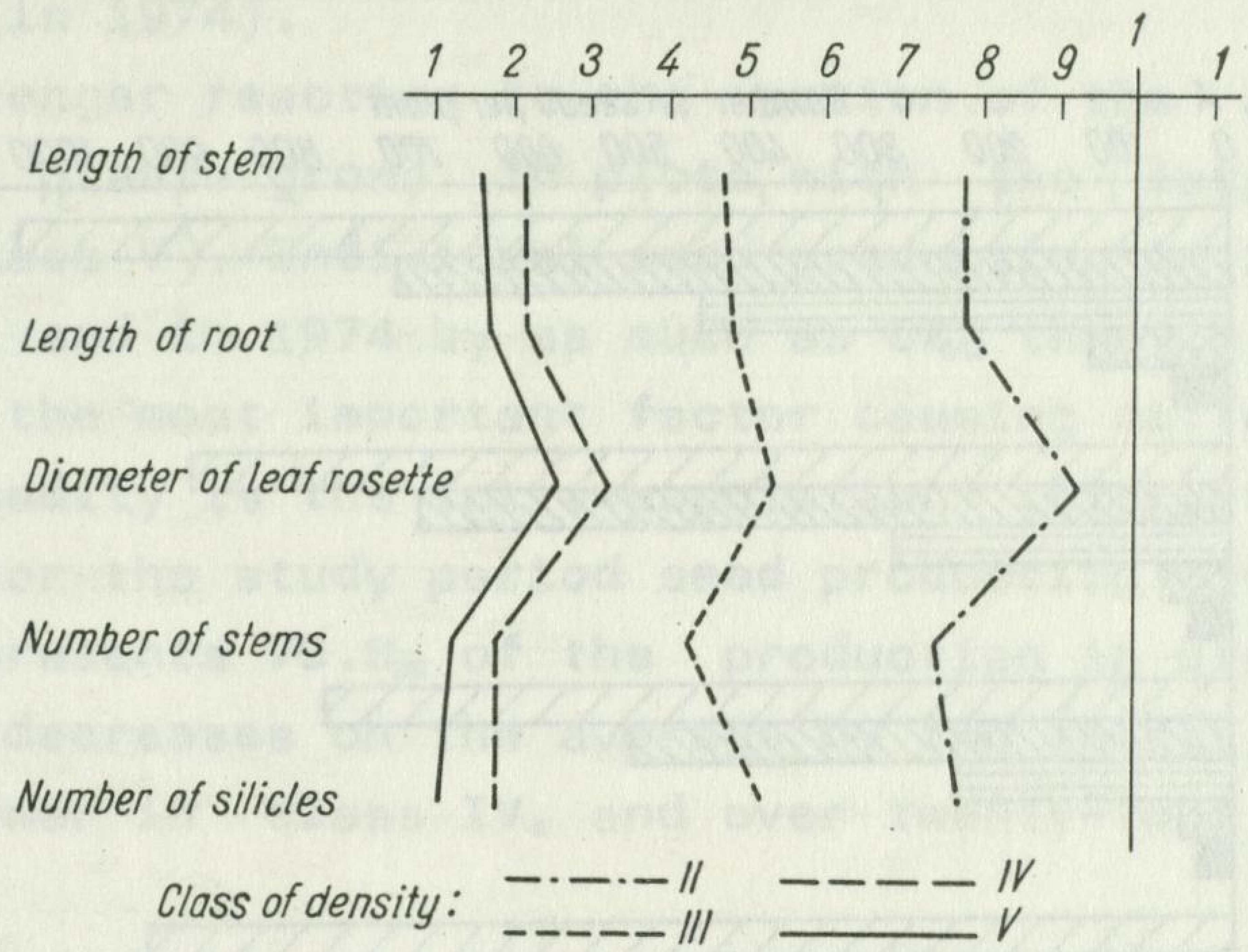

Fig. 6. Comparison of the morphological characters of individuals of density classes II-V (angular lines) with the characters of class I individuals (straight line) by Jentys-Szaferowa (1959) method
The diagram is based on average values for the study period. Density classes I-V as in Figure 1

of sensitivity of the characters studied to the conditions for growing which deteriorate with increasing density. A relatively less plastic character is the leaf-rosette diameter, although in this case, too, the differences between individuals of the different classes are significant at the 5% level of error risk.

All the characters are closely positively correlated, and no significant differences have been found in respect of the degree of correlation in the successive study years. The highest value of the correlation coefficient ($r = 0.94$ and $r = 0.96$) characterizes two character pairs: stalk length-root length, and number of stalks-number of silicles. A slightly weaker correlation has been found for the leaf-rosette diameter and the number of silicles. In this case also the value of the correlation coefficient is high, ranging from 0.86 to 0.91 in the particular years.

3.3. Effect of density on the fecundity of individuals

The fecundity of individuals expressed by the number of seeds produced (undamaged) varies, depending on the weather conditions during the growth and development of E. verna, length of life history and density (Fig. 7 A).

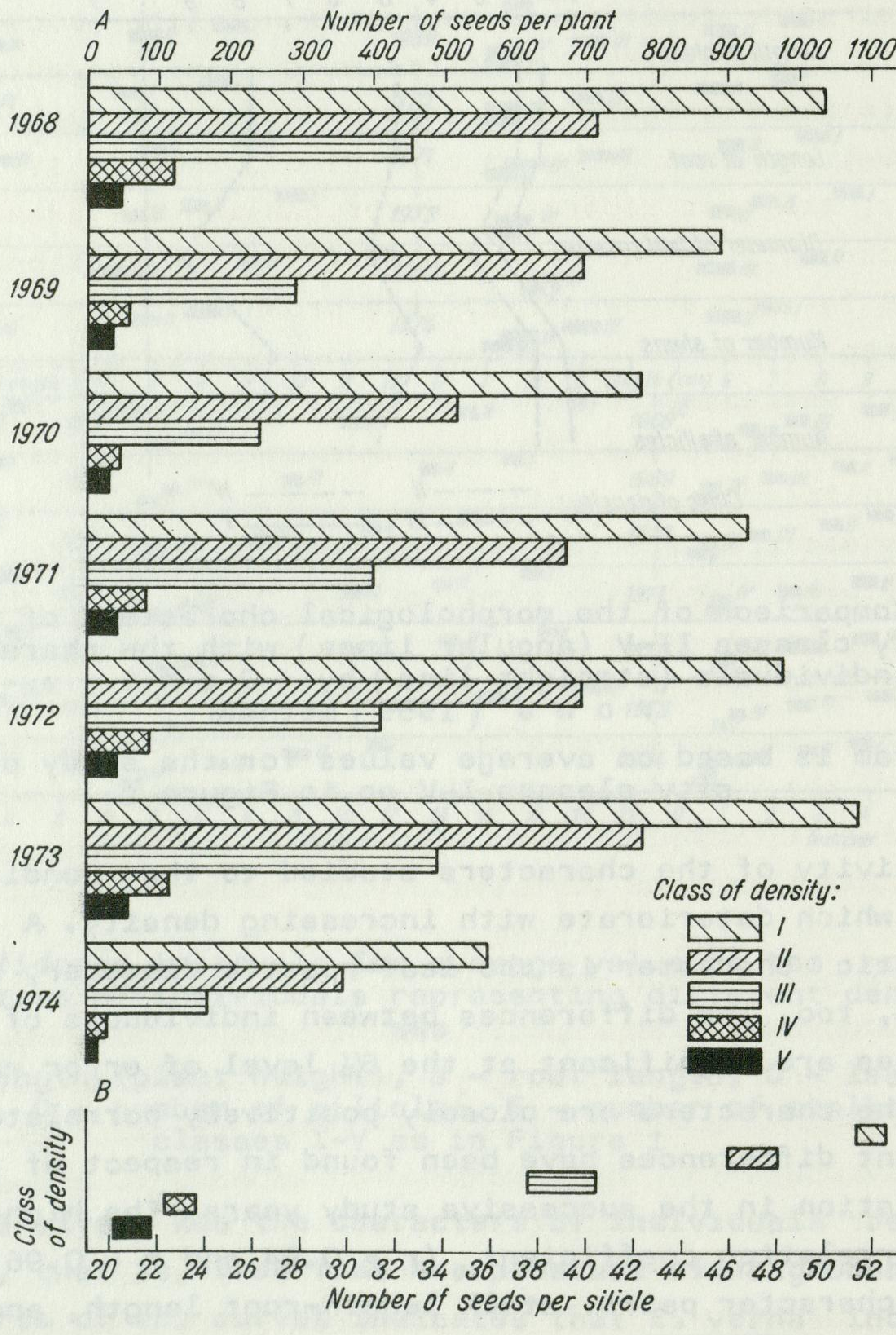

Fig. 7. Fecundity of individuals representing different density classes (A) and the average number of seeds in their silicles (B)
Density classes I–V as in Figure 1

If all the above factors are favourable, the fecundity is very high. Individuals free from the pressure of neighbours (class I) growing under favourable weather conditions and with an early germination date produce over 1000 seeds (in 1968 and 1973). The fecundity of this plant group was reduced by about 30% due to a shortening of the vegetative growth phase (in 1970), and by almost 50% as a result of a drought which accompanied the growth of E. verna (in 1974).

A yet stronger reaction to the action of the above factors was found in plants grown in plots with the largest number of seedlings (class V). Individual seed production in 1970 was lower by about 50%, and in 1974 by as much as 64% than in 1973.

However, the most important factor causing differences in individual fecundity is the intra-population interactions. While the average for the study period seed production by class II individuals represents 70.8% of the production in class I plots, in class III it decreases on the average by two thirds, and is thirteen times lower in class IV, and over twenty-four times lower in class V!

The highest absolute differences in seed production in plots of the different density classes were found in 1973, that is, under favourable climatic conditions and with a long life history of the population. However, density pressure has the strongest effect in a system of adverse environmental conditions. This is indicated by the results obtained for 1974: while individual fecundity in class III was 3.3 times lower than in class I, in class IV - already 22.4 times and in class V - as much as 37.2 times lower (Fig. 7 A).

The data given above indicate that the fecundity of individuals grown under different density conditions varies much more than do their size and habitus. Seed production is the resultant of the number of seeds in a silicle and the number of silicles produced by one individual. The former character appears to be as variable as the latter. The confidence intervals calculated for the mean value for the study period do not coincide or overlap even if neighbouring density classes are compared (Fig. 7 B). In the particular study years the number of seeds per an average silicle in analogous density classes differs insignificantly at the adopted level of error risk. It is not practically affected by weather conditions, and does not show any relationship to the length of the life history of E. verna.

On account of the problems included in the scope of the research undertaken the possibility of precisely assessing the effect of density on the fecundity of individuals becomes very important. The assessment was carried out on the basis of data from specially selected plots differing from each other each year exactly by 5 seedlings in the interval of 1 to 56. The correlation coefficient, calculated on the basis of the average, for the study period, individual diaspore production (r = -0.99) indicates a very close, negative correlation of both characters. The value of the regression coefficient shows, that with an increase in density by one seedling per 0.01 m^2 adult individuals will produce fewer seeds by 15.8 than individuals free from the pressure of neighbours (Fig. 8).

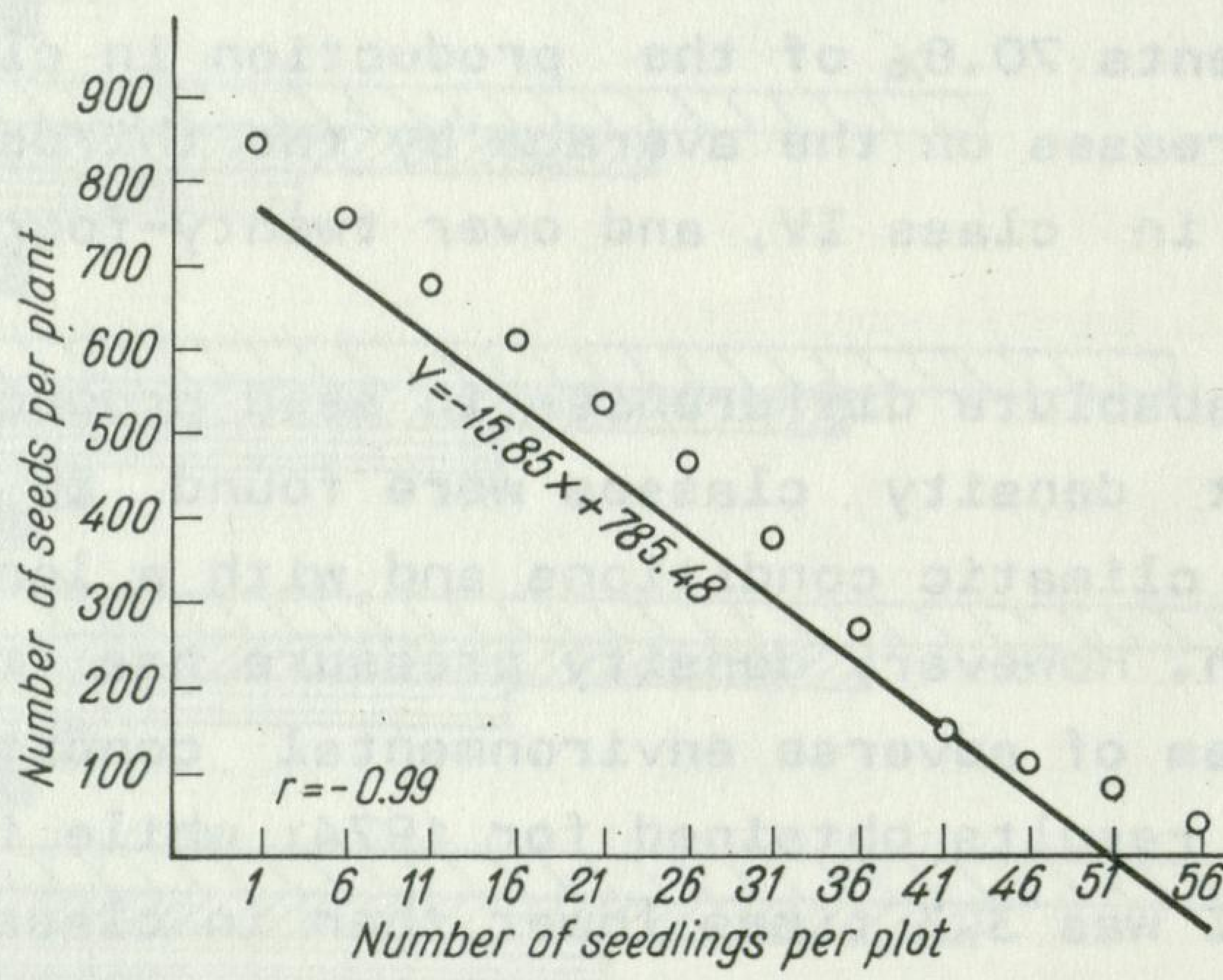

Fig. 8. Correlation between seedling density and individual fecundity

3.4. Contribution of individuals of different density classes to the total seed production

The overall contribution of individuals representing the different density classes to the total production of seeds is determined by their fecundity and numbers. In the seedling phase, density class I individuals form each year the least numerous group. Their proportion does not exceed 4% of all the seedlings taken into account in the present study. Class IV and class V individuals represented a considerable, although different each year, percentage; their total contribution amounted on an average to 56.4% (Fig. 9 A).

In the fruiting season the population structure is subject to conspicuous changes. The proportion of class I individuals is over twice as large, but they continue to be the least numerous fraction, not exceeding 8% of all individuals. The percentage of class

II individuals was noticeably higher; in the first five years they dominated numerically over the individuals of the other classes. But the proportion of individuals of classes IV and V was much smaller: they constituted jointly 32.5% (Fig. 9 B).

The contribution of the different groups of individuals to the total production of diaspores is not proportionate to their numbers, especially to their initial numbers (in the seedling phase). Individuals of density class II account on an average for as much as 60.4% of the total seed production. The joint contribution of individuals of classes IV and V is as low as 7.5%, being lower by over 3% than that of class I individuals (Fig. 9 C).

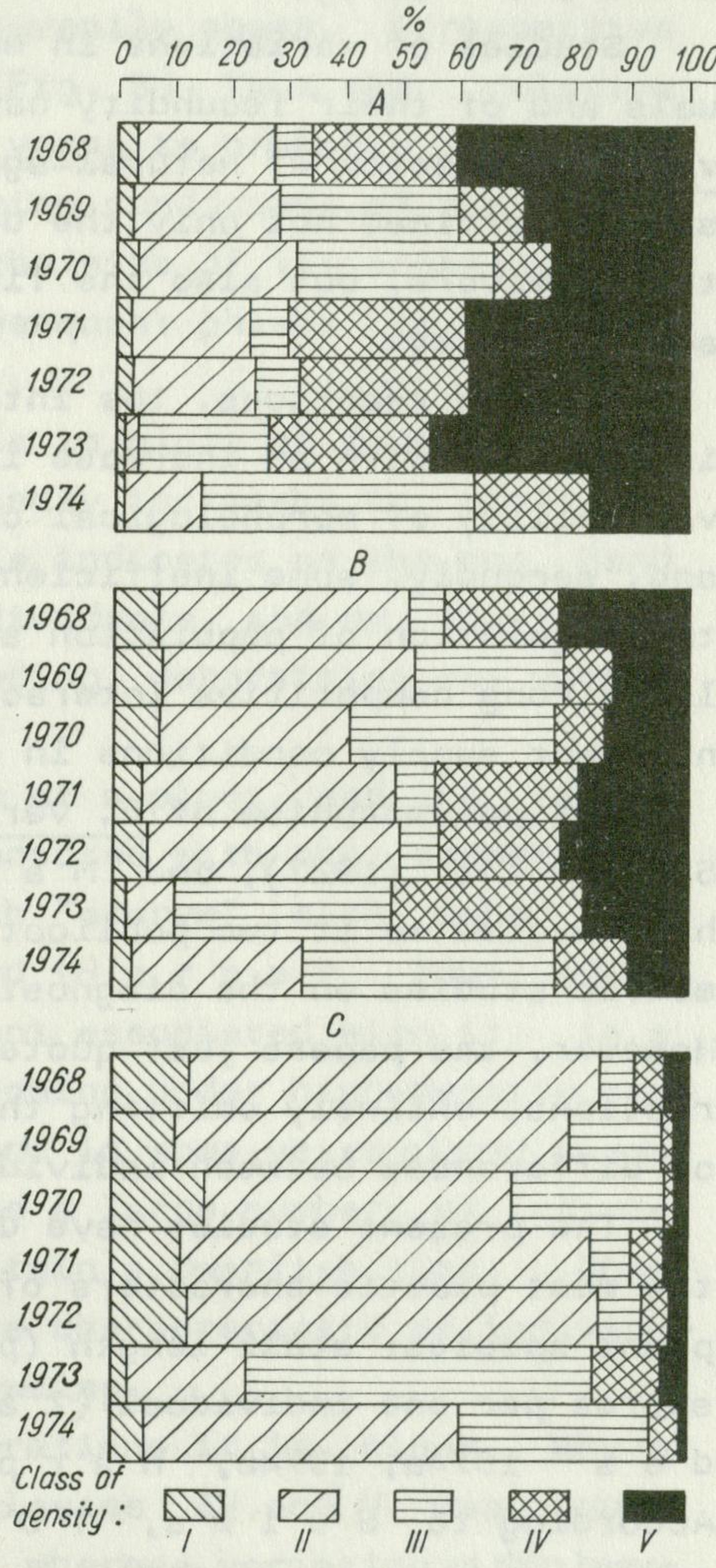

Fig. 9. Relationships between individuals of the particular density classes

A - proportion of individuals in the seedling phase, B - proportion of individuals in the fruiting phase (in either case 100% was the joint number of individuals in the plots taken into account in the study), C - contribution of individuals belonging to different density classes to the total production of seeds. Density classes as in Figure 1

4. DISCUSSION

The first paper of the present series has shown that a growth in the density of seedlings in an E. verna population causes an increase in mortality, acceleration of the rate of phenological development, as well as a decrease of the proportion of individuals attaining generative phases. Thus the chance to survive and reproduce of the different individuals, and thereby their position in the population are to a considerable extent determined by the distances separating individuals in the seedling phase (S y m o n i d e s 1983).

Studies of variations in morphological characters of individuals and of their fecundity have confirmed the presence in the E. verna population of natural aggregations in which the initial density determined not only the death rate and development rate of the survivors, but also the final size of their vegetative organs and fecundity.

Plastic reactions, the intensity of which increases in E. verna individuals with an increase in density indicate, firstly, a great variability of morphological characters of the species under study, and, secondly, some inefficiency in the mechanisms responsible for the regulation of population abundance through mortality and, thirdly, strong competitive interactions between individuals under low nutrient supply conditions in the biotope.

The polymorphism of E. verna has been noticed already by S c h u l z (1927), and M a t u s z k i e w i c z (1948a, 1948b) has devoted to it two publications of the type of taxonomic-biometric studies on the diagnostic value of some of the characters. However, the papers just quoted concentrated on geographical variations, entirely omitting the effect of other non-genetic sources of differences between individuals.

The present studies have demonstrated that the following are the most plastic characters of E. verna, as well as of many other plant species: stalk length (plant height) and the number of diaspores per one individual (Z a r z y c k i 1965, S y m o n i d e s 1974a, 1974b, H a r p e r 1977, S t a s i a k 1978). According to S u l m a, T o k a r z and W i e r z c h o w s k a - R e n k e (1967), a great variability of the above characters is particularly characteristic of plants with a wide ecological scale. Covariant with the height of a plant appear to be the remaining characters: root length, leaf-rosette diameter, number of stalks and number of fruits.

Individuals growing under different density conditions clearly differ in stalk length already in the vegetative growth phase (Fig. 1). The differences grow gradually until the end of the life of the population, though there is a simultaneous gradual decrease of differences in the density of the particular aggregations (Fig.

2). This finding indicates that the final size attained by a plant is primarily determined by the conditions of its growth in the earliest phase of its life. This conclusion is also supported by the analysis of the relative growth rate: a plant realizes over 60% of its increment already in the juvenile phase, irrespective of the density under which it grows (Fig. 3). Thus the relative growth rate in the ontogenesis of E. verna is probably determined genetically. But dependent on the living conditions of the plant early in its life is its size (and the size of its organs), this dependence continuing also in the subsequent phases of the life history.

The height of plants varies little in plots of density classes I and II, but its variability markedly increases in plots of the remaining classes (Fig. 4). This indicates on the one hand small genetic differences between individuals, and on the other hand a significant effect of overcrowding, determining the variability of the character in question.

The effect of density on the size of a plant, and the variability of this plant is no doubt connected with the competitive interactions between individuals which "starve" each other if the capacity of the biotope is limited (H a r p e r 1961, 1964). Due to competition and undernourishment associated with it, in a considerable number of individuals growing under high-density conditions (plots of classes IV and V, and in some years also of class III) the stalk does not develop, while a large number of individuals living under such conditions attain a dwarfish size. Only a small number of them attain the size characteristic of individuals free from the pressure of overcrowding.

In the light of the above considerations it is clear why a statistical individual in plots of classes IV and V was much shorter than in class I and II plots, whereas variation within heavily overcrowded aggregations was greater than that in plots with a small number of individuals. This finding confirms the thesis put forward by Japanese ecologists that a population forms an integrated system, whereas the possibility of growing of the individuals depend on the resources disposed of by the population as a whole (K i r a, O g a w a and S a g a z a k i 1953, S h i n o z a k i and K i r a 1956, Y o d a, K i r a and H a z u m i 1957).

In the case of an E. verna population consisting of many spatially delimited aggregations it may be stated that it is the aggregations of individuals that form integrated, independently functioning systems. Within their boundaries nutrients are shared, and differences arise between individuals which compete for these nutrients if their quantity is smaller than the expected requirement of the specific number of individuals making up an aggregation.

The significant covariation, found during the present studies, of the morphological characters analysed may be determined genetically or be the result of an independent reaction of organs to the conditions under which the individual is growing. Depending on the density, length of the life history and weather conditions, the size of the vegetative organs of the plants varied, and so did the habitus of the individuals and their diaspore production.

The wealth of plastic reactions in plants which reproduce generatively has many times been reported in the relevant literature (P a l m b l a d 1968, S y m o n i d e s 1974a, W i l k o ń-M i c h a l s k a 1976, F a l i ń s k a 1977). The close relationship has also been known between population density and individual production of diaspores (S a l i s b u r y 1942, H o d g s o n and B l a c k m a n 1957, S y m o n i d e s 1979b, L e e and B a z z a z 1980, W e i n e r 1980, L a w 1981).

In E. verna the relationship between the density and fecundity of an individual is particularly strongly marked (Figs. 7, 8). Seed production is the resultant of several characters: number of stalks, number of silicles on a stalk and number of seeds in a silicle, each of which is negatively correlated with density. Bigger, more branched plants produced each year a larger number of fruits and seeds than did small ones with only a single stalk. Thus both the size of the vegetative organs and the fecundity of E. verna plants are controlled by density-dependent factors (B a r k h a m 1980).

The size of the leaf-rosette seems to play a particular role. It is an index of the size of the assimilation apparatus on which the amount of the assimilated energy depends to a large extent. If a more or less constant percentage is assumed of bound energy that the plants utilize for their growth, current maintenance and reproduction, then the relationship between leaf-rosette size and individual fecundity becomes understandable. This relationship has also been found in other rosette-forming plants, e.g., Dipsacus sylvestris Huds. (W e r n e r 1977), Senecio jacobaea L.

(Meijden and Waals-Kooi 1979), Tragopogon heterospermus Schweigg. and Androsace septentrionalis L. (Symonides 1979a).

Results from studies of variations in morphological characters and especially of the variability of the fecundity of E. verna, depending on seedling density indicate strong competitive interactions between individuals from the beginning of their life. They are usually strongly marked if the competitive relationship is between individuals of the same species and the same generation, thus individuals with very similar requirements with regard to the resources of the biotope (Rabotnov 1950, Sukačev 1953, McNaughton and Wolf 1970).

In E. verna the competition between individuals in the earliest life phase is intensified due to the fact that the growth of seedlings is almost simultaneous and their size is almost identical (Symonides 1983). Obviously, even small differences in the germination date, and small variations of the size of seedlings may have caused within the same aggregations differences in the chance of the individuals to survive and reproduce (Ross and Harper 1972, Symonides 1978).

A seemingly surprising, and therefore requiring clarification is the presence of significant differences in the size and fecundity of individuals representing density classes I and II. It indicates certain limitations in the free growth and development of E. verna already at low levels of density of the individuals inhabiting the same area, that is, when the average distance between seedlings is still 2-4 cm. This distance is long enough not to permit direct contact between seedlings, but when the leaf-rosettes have formed, i.e., several days after the germination, the leaves of neighbouring individuals in class II plots overlap in 27.2%. This is because the distance between the individuals (on an average 3 cm from the middle of the rosette) is smaller than the rosette diameter (on an average 3.6 cm). The statement may thus be ventured that the assimilative capacity of individuals in plots of density class II is limited by impeded light flow to the leaves, and as a result their growth is also limited, relative to that of individuals free from the effect of neighbours.

In higher density classes the competition between individuals is probably caused also by a low nutrient content in the soils (Gore 1961, Harper and Gajic 1961, Marshall

1965, Willis 1965, White and Harper 1970). This will become clear when the fact is taken into account that the content of humus in the soils of the study areas is only 0.23% (Symonides 1974b). From this follows that the supply of nutrients is not sufficient for a large number of individuals concentrated in a small area, hence the increased "competitive pressure" between individuals with an increase in density.

A detailed analysis of the relationship between the density of seedlings and individual fecundity has shown, however, that a close negative correlation is maintained only to a certain threshold density. If density exceeds the level of 46 seedlings per 0.01 m^2, the relationship between the two characters loses its linear nature (Fig. 8).

Apart from the density-dependent factors, the size of the vegetative organs and the fecundity of E. verna individuals are also under the influence of the length of the vegetative growth period: if the life history is relatively long, then plants are bigger, more branched and produce more seeds. It should be noted, however, that the length of the life history of E. verna, though being primarily determined by the date of seed germination, may to some extent depend on density (Symonides 1983).

Caswell and Werner (1978) attribute the relationship between the duration of the life history and the size and fecundity of plants to differences in the amount of nutrients assimilated which is larger when the life history is longer. In addition, Harper and White (1974) explain that annuals attain generative phases without the action of any environmental stimuli, and only with a long growth period can they be "fully exploited", that is, can produce large numbers of seeds.

Climatic conditions probably also contribute to the variations, in the different year, in individual fecundity in plants of analogous density classes. Unfortunately, because of changing weather conditions during the growth and development of E. verna, it is difficult to demonstrate causal relationships between air-temperature systems and the amount of precipitation, and the size of the vegetative organs and fecundity of individuals. A negative effect has only been found of a prolonged drought in 1974 on both the growth and seed production of E. verna.

To sum up, the studies have shown that the primary spatial structure of a population - spatial structure of seedlings - is a significant factor causing differences in the size and fecundity of individuals. As a result of its effect, the overall contribution of individuals representing different classes of density to the total production of seeds is not proportionate to their numbers (Fig. 9). The results also suggest an uneven contribution of individuals to the real fecundity of the population if the ability to germinate were independent of the density of the plants that have produced them, and if each viable seed had the same chance to germinate. These problems will be dealt with in the last paper of the present series (S y m o n i d e s - in press).

5. SUMMARY

The present paper represents part of wide-scope studies concerned with the role of intra-population interactions in the regulation of numbers in an E. verna population. The preceding paper discussed the effect of interactions between individuals on the growth rate and survival (S y m o n i d e s 1983). The subject of the present paper is an analysis of the growth rate, morphological characters and fecundity of individuals growing under different density conditions.

The starting point in the studies was the following assumptions: (1) the intensity of interactions between even-aged individuals is to a large extent the function of the distances separating them, (2) differences between individuals lead to an uneven sharing of biotope resources, thus being a significant element of population stability (Ł o m n i c k i 1980), (3) different weather conditions may weaken or intensify intra-population interactions.

The studies were carried out in the years 1968-1974 in a patch of Festuco-Koelerietum glauceae. For the purpose of the studies five seedling density classes were taken into account: class I - 1-2, class II - 5-10, class III - 15-30, class IV - 35-50, class V 55 or more seedlings per 0.01 m^2.

Measurements of the height of individuals for the assessment of the rate of their seasonal growth were made in the seedling, vegetative growth, budding, flowering, fruiting and seed-disseminating phases. Taken into account in the analysis of morphological characters including - in addition to plant height - root length, leaf-rosette diameter, number of stalks and number of silicles, were only individuals in the fruiting phase. A sample always con-

sisted of 100 randomly selected individuals from each density class. The fecundity of the plants was determined on the basis of the product of the number of silicles and the number of seeds in an average silicle.

The studies have shown that in the seedling phase individuals do not practically differ in their size, but already from the next phase - the lower the density, the higher the plants. Differences in the height of individuals of the different density classes are conspicuous each year, regardless of the length of the life history and weather conditions (Fig. 1). They persist until the end of the life of the population, in spite of a gradual decrease in density differences, caused by a higher mortality in plots of the higher density classes (Fig. 2). The highest relative growth rate is seen at an early stage of the life history of plants, and it does not then show any relationship with their density (Fig. 3). Differences in the size of individuals within the aggregations depend on the intensity of interactions between plants, the stronger the interactions, the greater the differences (Fig. 4).

As a result of intra-population interactions, plants growing at a high density are shorter, and they have a shorter root, smaller leaf-rosette diameter, and fewer stalks and silicles than plants free from the pressure of neighbours (Fig. 5). All characters are simultaneously subject to the effect of factors from outside the population, but the differences caused by the competitive interactions between individuals are not blurred (Fig. 6).

Particularly striking is the relationship between seedling density and individual fecundity (Fig. 7). A growth in density by one seedling causes a decrease in individual production by 15.8 seeds (Fig. 8). As a result, individuals growing in heavily crowded aggregations produce jointly fewer seeds than in plots sparsely overgrown with seedlings (Fig. 9).

To sum up, the study has demonstrated a significant effect of interactions between individuals on their size and fecundity. Aggregations of individuals form ecological systems, functioning independently, in which nutrient supply is shared, and there is competition there between individuals which differ in size and fecundity (cf. Yoda, Kira and Hozumi 1957, McNaughton and Wolf 1970, Harper 1977).

6. POLISH SUMMARY

Praca jest częścią szerszych studiów poświęconych roli oddziaływań wewnątrzpopulacyjnych w regulacji liczebności populacji E. verna. W poprzedniej publikacji omówiono wpływ interakcji między osobnikami na tempo ich rozwoju i przeżywalność (S y m o n i d e s 1983). Przedmiotem prezentowanej pracy jest natomiast analiza tempa wzrostu, cech morfologicznych i płodności osobników wyrosłych w odmiennych warunkach zagęszczenia.

Punktem wyjścia w badaniach były następujące założenia: 1) siła wzajemnych oddziaływań między osobnikami jednego wieku jest w znacznym stopniu funkcją dzielących je odległości, 2) zróżnicowanie między osobnikami powoduje w efekcie nierówny podział zasobów biotopu, jest więc istotnym elementem stabilności populacji (Ł o m n i c k i 1980), 3) odmienne warunki pogodowe mogą osłabiać lub wzmacniać interakcje wewnątrzpopulacyjne.

Badania prowadzono w latach 1968-1974 w płacie Festuco-Koelerietum glaucae. Ze względu na ich cel uwzględniono 5 klas zagęszczenia siewek obejmujących: I klasa - 1-2, II klasa - 5-10, III klasa - 15-30, IV klasa - 35-50, V klasa 55 lub więcej siewek na powierzchni 0,01 m^2.

Pomiar wysokości osobników dla oceny tempa ich sezonowego wzrostu przeprowadzono w fazie siewki, wzrostu wegetatywnego, pączkowania, kwitnienia, owocowania i rozsiewania nasion. Analizą cech morfologicznych, uwzględniających - oprócz wysokości rośliny - długość korzenia, średnicę rozetki liściowej, liczbę łodyg i liczbę łuszczynek, objęto wyłącznie osobniki w fazie owocowania. Próbę stanowiło zawsze 100 losowo wyznaczonych osobników z każdej klasy zagęszczenia. Płodność roślin ustalono na podstawie iloczynu liczby łuszczynek i liczby nasion w przeciętnej łuszczynce.

Badania wykazały, że w fazie siewki praktycznie nie istnieje zróżnicowanie wielkości osobników. Już od następnej fazy osobniki są jednak tym wyższe, im mniejsze było zagęszczenie siewek. Różnice w wysokości osobników poszczególnych klas zagęszczenia są wyraźne w każdym roku, niezależnie od długotrwałości cyklu i warunków pogodowych (rys. 1). Utrzymują się one do końca życia populacji pomimo stopniowego zmniejszania się różnic w zagęszczeniu, spowodowanego wyższą śmiertelnością na poletkach wysokich klas zagęszczeń (rys. 2). Względne tempo wzrostu jest najwyższe we wczesnym okresie życia roślin i nie wykazuje wtedy związku z ich zagęszczeniem (rys. 3). Zróżnicowanie wielkości osobników w obrębie poszczególnych skupisk jest tym wyższe, im silniej oddziałują na siebie badane rośliny (rys. 4).

Intereakcje wewnątrzpopulacyjne powodują, że rośliny wyrosłe w dużym zagęszczeniu są niższe, mają krótszy korzeń, mniejszą rozetkę liściową, mniejszą liczbę łodyg i łuszczynek niż wolne od presji sąsiadów (rys. 5). Wszystkie cechy podlegają równocześnie wpływom czynników zewnętrznych w stosunku do populacji, tym niemniej nie zacierają one różnic wywołanych konkurencyjnym oddziaływaniem między osobnikami (rys. 6).

Szczególnie jaskrawo zaznacza się związek między zagęszczeniem siewek a płodnością osobników (rys. 7). Wzrost zagęszczenia o jedną siewkę powoduje spadek osobniczej produkcji o 15,8 nasion (rys. 8). Wskutek tego osobniki w silnie zagęszczonych skupiskach produkują łącznie mniej nasion niż na poletkach skąpo porośniętych siewkami (rys. 9).

Reasumując, badania wykazały istotny wpływ oddziaływań między osobnikami na ich wielkość i płodność. Poszczególne skupiska osobników tworzą samodzielnie funkcjonujące systemy ekologiczne, w których dokonuje się podział zasobów, konkurencja między osobnikami oraz różnicowanie ich wielkości i płodności (por. Yoda, Kira i Hozumi 1957, McNaughton i Wolf 1970, Harper 1977).

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