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EFFECT OF SEED SIZE, DENSITY AND DEPTH OF SOWING ON THE GERMINATION AND SURVIVAL OF PSAMMOPHYTE SEEDLINGS

ABSTRACT: Under laboratory conditions the relationship was studied between the seed size, the density and depth of sowing, and the germinating process and its time, the fixing of seedlings and their survival in *Corynephorus canescens* (L.) P. B., *Spergula vernalis* Willd. and *Androsace septentrionalis* L. The factors enumerated above appeared not to affect the germinating capacity and power, but they were found to have an influence on the rate of growth of the germs (thus also, indirectly, on the rate of seedling growth), and on the survival of germs and seedlings. As a result of a high rate mortality of germs at high densities, the numbers of seedling survivors were similar, regardless of the number of seeds sown.

KEY WORDS: Psammophyte seedlings, seed size, sowing density, sowing depth, germinating capacity, seedling survival, laboratory investigations.

Contents

1. INTRODUCTION

Many studies on the survival of seedlings, carried out in the field and under culture conditions, have proved that during the early plant growth stages the rate of mortality is high.

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Many papers indicate a high degree of correlation between the mortality of seedlings and their density (Marschall and Jain 1969, Mathews and Westlake 1969, White and Harper 1970, Ross and Harper 1972), the dying seedlings being first of all poorly developed individuals, weak from the beginning of their life (Morozow 1953, Sukačev 1953). It has also been found that more likely to survive, especially at high density levels, are those seedlings which were the first to appear in a given population; this is probably associated with their having the possibility to occupy a larger biological space than in the case of seedlings, the growth of which takes place at a later time (Cavers and Harper 1967, Ross and Harper 1972). It is not quite clear, however, what causes the differences in the time of emergence of the individual seedlings in a population, determining their further fate.

The aim of the experiments presented in this paper was to find out whether an earlier or later emergence of a seedling is entirely a matter of chance, or the result of the influence of some not known well factors. In the study the effect, direct or indirect, was assumed to be possible of the seed size, and the density and depth of sowing. A further objective of the study was to establish a possible effect of the factors named above on the germination and survival of seedlings.

The problems put forward in the paper relate to observations, conducted for several years, on the mortality of seedlings in natural psammophyte populations (Symonides 1977), which have revealed, among other things, a close relationship between the density and emergence time of seedlings, and their survival, this relationship being particularly evident in *Corynephorus canescens* (L.) P. B., *Spergula vernalis* Willd., and *Androsace septentrionalis* L. These species were selected for the subsequent studies, as specified in the title of the present paper.

2. METHODS

The starting point in the experiments was the assumption that the absolute number of seeds and germs in the soil exceeds the number of the seedlings that emerge, because some of the germs probably die before emerging above the ground. It was for this reason that at first an estimation of the germinating capacity of the seeds in Petri dishes was made. In each of the dishes 100 and 300 specially selected – large and small – seeds[1] were sown in four replications for each species. As soon as the first seed had germinated, the counting of germs was started and continued every 24 hours for 30 days. For each variant of seed size and density the average germinating capacity was then calculated, and the per cent germination in the successive 24–hours' intervals, relative to the total number of germs.

The selection of *Spergula vernalis* and *Androsace septentrionalis* seeds was made by sieving them through a series of sieves with a gradually decreasing mesh diameter: 1.2 mm, 1.0 mm, 0.75 mm, 0.6 mm, 0.4 mm. Seeds of both species were considered "large" if they remained on the sieve with a mesh diameter of 1.0 mm, "small" – on the sieve with a mesh diameter of 0.6 mm. Because of their elongate shape, the caryopses of *Corynephorus canescens* were

[1] The term "seed" is in this paper used in a broad sense to include also the caryopses of *Corynephorus canescens*.

measured directly: those whose length exceeded 5 mm were considered large, those below 4 mm in length – small.

The objective of the second stage of experiments was to investigate the rate of emergence of the seedlings, and of their survival depending on the size of the seeds sown, and on the density and depth of sowing. The seeds were sown at regular intervals into soil (dune sands) placed in pots of the size 20 × 30 cm, each of them divided by inner partitions into six equal-sized plots, each 100 cm^2 in area. For both the large and the small seeds 3 density variants were used: 100, 200 and 400 seeds per plot, and 2 depth variants: 0.5 and 3.0 cm. Each of the sowing density and depth variants and the seed sizes was replicated three times. Thus for each species the total number of "plots" investigated was 36.

The time of sowing was adjusted to the natural growth rhythmicity of the particular species: seeds of *Androsace septentrionalis* were sown in March (after a previous stratification for 7 days at temperatures from 0 to -2°C), and those of the other species – in August. The experiments were carried out at room temperature in the laboratory.

For two months all seedlings emerging and dying were counted. After the termination of the experiments the seedlings were removed from the plots and measured to the nearest 1 mm. The above-ground parts and roots were measured separately.

For each plot the following were calculated:

1. percentage of seedlings found, relative to the number of seeds sown;

2. percentage of seedlings which emerged on the successive days of the experiment, relative to the total number of seedlings found;

3. percentage of dead seedlings, relative to the number of seedlings that emerged on the particular experimental day;

4. average seedling-size: root length and the height of the above-ground parts – for *Corynephorus canescens* and *Spergula vernalis* seedlings, and the rosette diameter – for *Androsace septentrionalis* seedlings.

In a further part of this paper the mean values are presented from similar variants of seed size, density of sowing and depth of sowing.

3. RESULTS

Figure 1 illustrates the germinating capacity and the process of seed germination in Petri dishes. The data indicate several regularities: (1) small seeds germinated 1–2 days earlier than the large ones; (2) for large seeds a much higher per cent germination was recorded than for the small seeds; (3) the density of seeds sown had no significant effect on the per cent germination and the course of the germinating process; (4) the germination curves for the species compared are similar, in spite of the fact that their total germination times differed.

Under soil conditions, seedlings derived from large seeds emerged earlier than did those which germinated from small seeds (Figs. 2–4). This regularity applies to all species and to all variants of density of the seeds sown, and depth of sowing. However, greater differences in the time of emergence of the seedlings, both of the first to appear and of the majority of seedlings, could be seen when a deeper sowing of large and small seeds had been applied.

At a given sowing depth seedlings emerged earlier in plots with a lower sowing density (100 and 200 seeds per 100 cm^2) than in those with the highest density used (400 seeds per 100 cm^2), regardless of the size of the seeds.

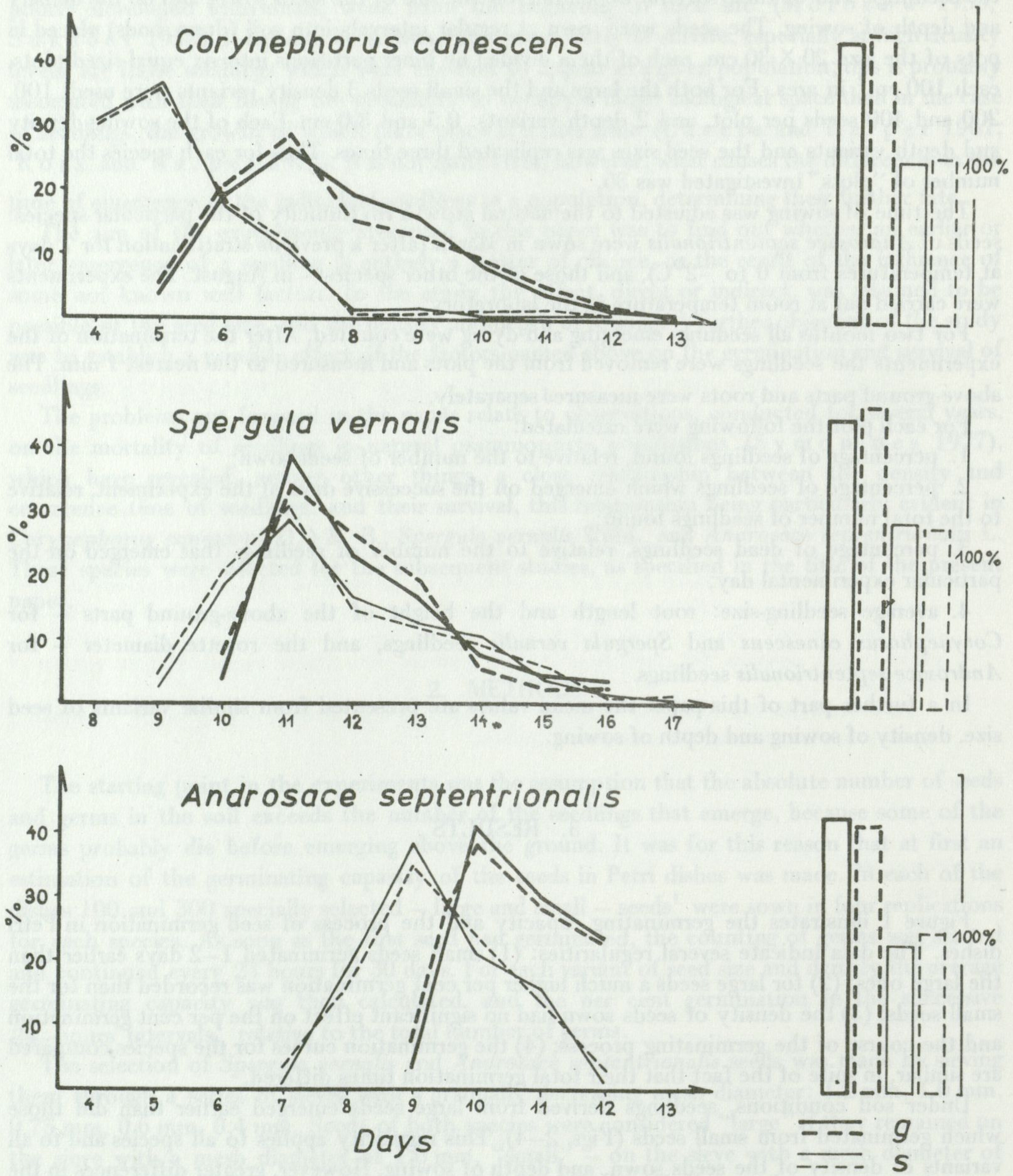

Fig. 1. Seed germination in Petri dishes

Left side — germinating process, 100% number of germs. Right side — germination capacity, 100% — number of seeds sown. *g* — large seeds, *s* small seeds. Sowing density: continuous lines — 400 seeds, broken lines — 100 seeds

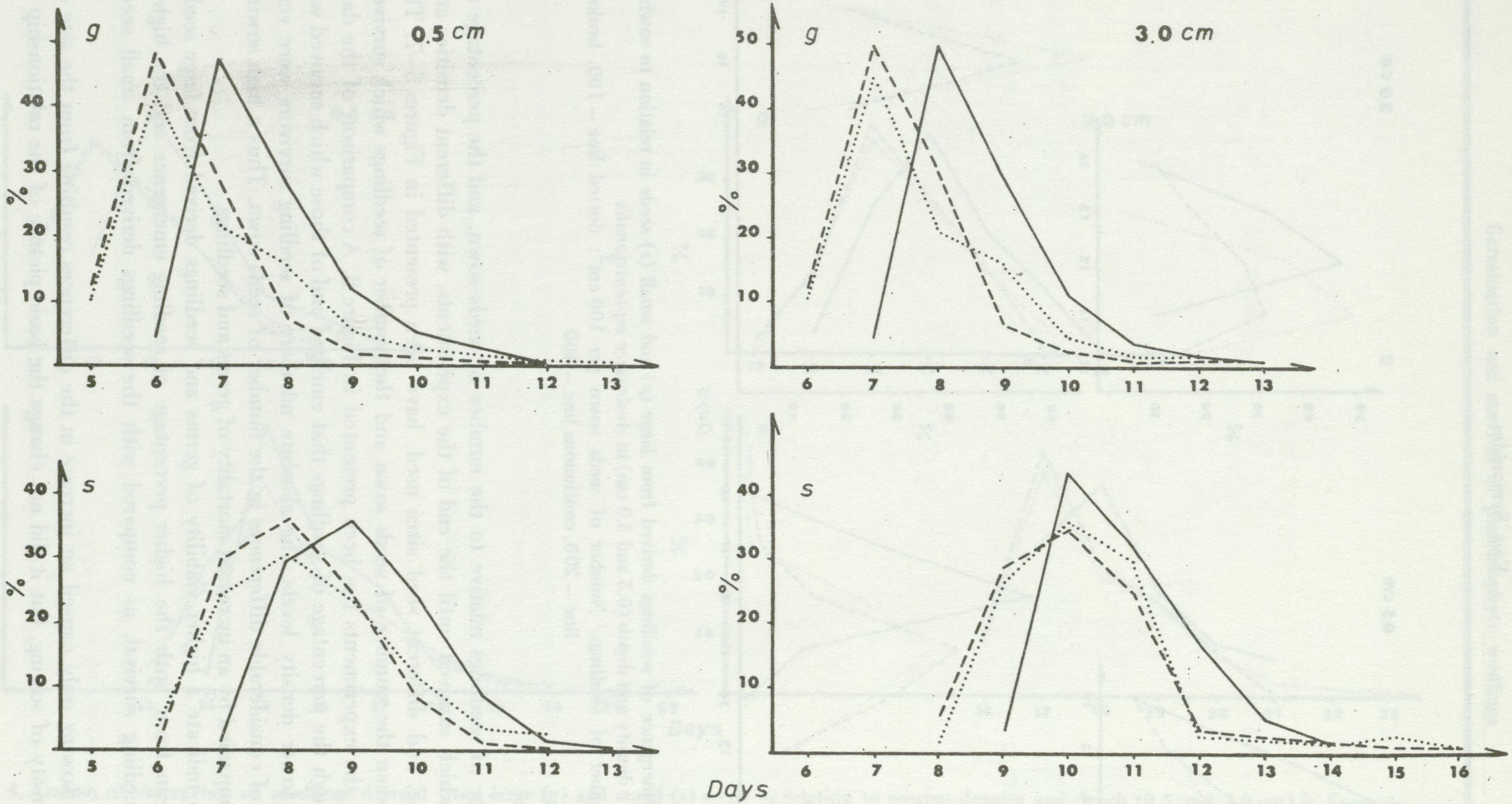

Fig. 2. Course of emergence of seedlings derived from large (*g*) and from small (*s*) seeds in relation to sowing density and depth (0.5 and 3.0 cm) in *Corynephorus canescens*

100% – total number of seedlings. Number of seeds sown per 100 cm^2: dotted line – 100, broken line – 200, continuous line – 400

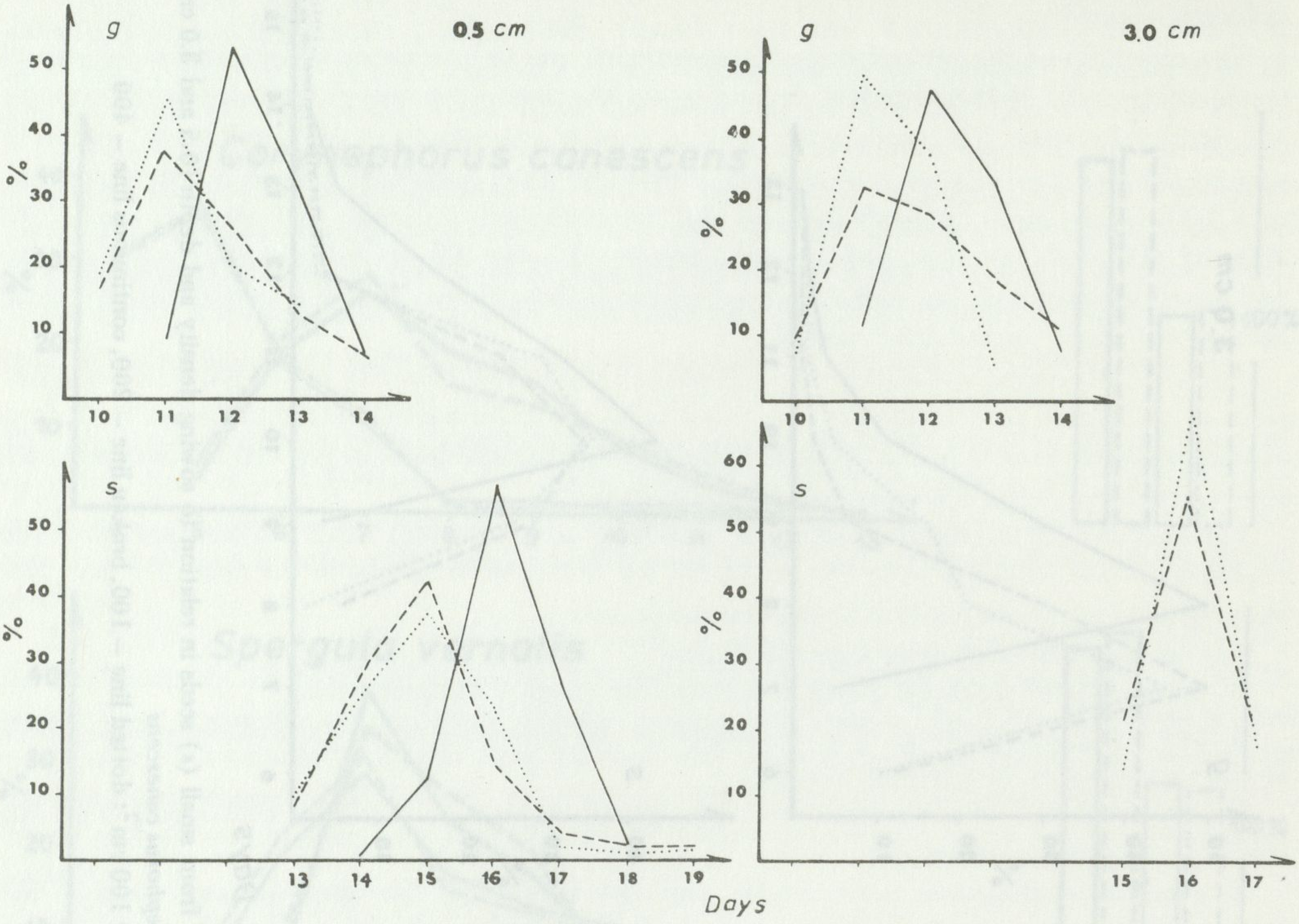

Fig. 3. Course of emergence of seedlings derived from large (*g*) and small (*s*) seeds in relation to sowing density and depth (0.5 and 3.0 cm) in *Androsace septentrionalis*
100% – total number of seedlings. Number of seeds sown per 100 cm^2: dotted line – 100, broken line – 200, continuous line – 400

The percentage of seedlings relative to the number of seeds sown, and the percentage of those seedlings which survived until the end of the experiments, with different densities and depths of sowing, and different seed sizes used, have been presented in Figures 5–7. The relationship between the number of seeds sown and the number of seedlings which survived until the end of the experiments has been presented in Figure 8. A comparison of the data shows that although the percentage of seedlings that emerged and of those which survived was much higher at lower density levels, the absolute numbers of seedling survivors were very similar, in spite of considerable differences in the number of seeds sown. Thus a high sowing density was accompanied by an increased mortality of germs and seedlings.

The data also indicate a higher viability of germs and seedlings derived from large seeds, which can be seen from both the higher percentage of seedling emergence and the higher percentage of seedling survival, as compared with the seedlings derived from small seeds (Figs. 5–7).

The depth of sowing only caused an increase in the differences resulting from the size of seeds and the density of sowing, but it did not change the basic picture of the relationship in question.

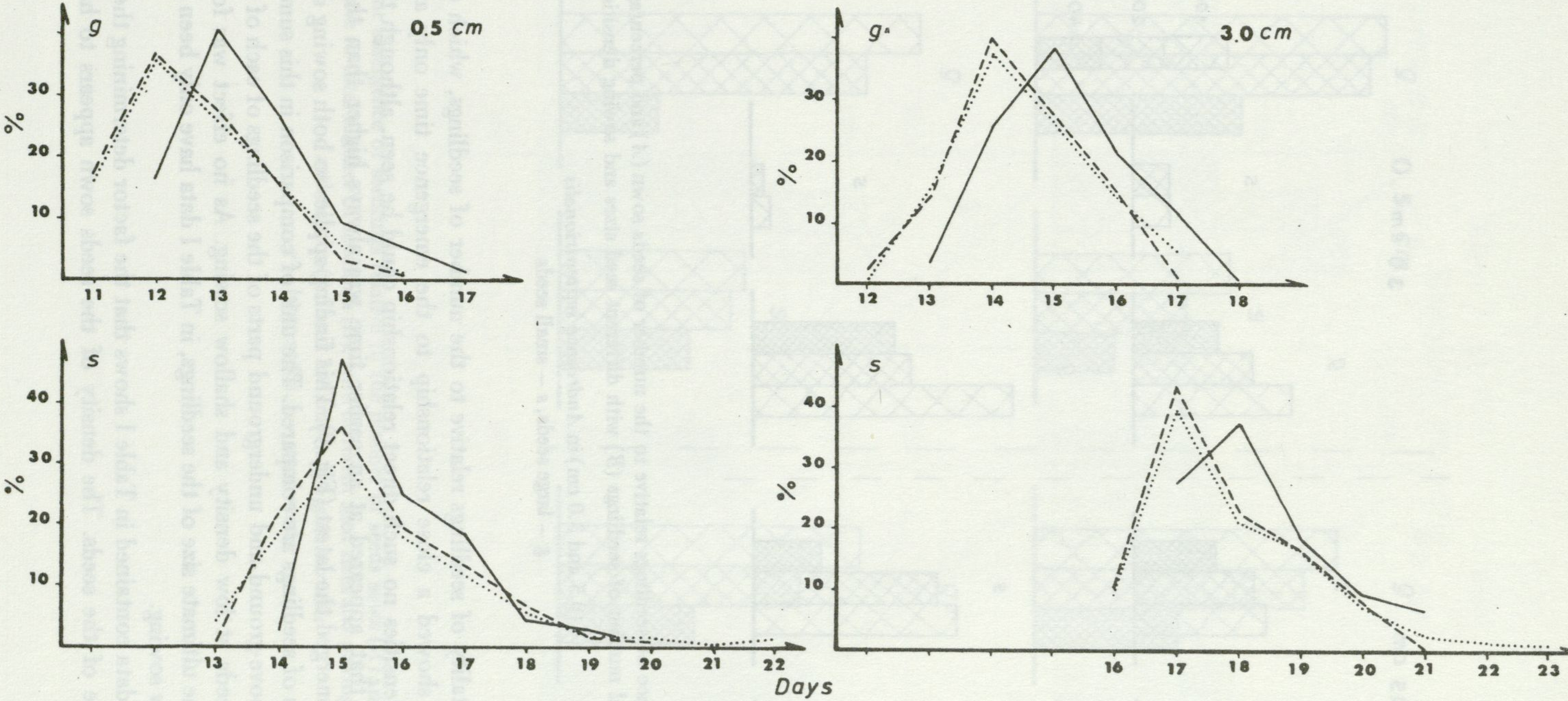

Fig. 4. Course of emergence of seedlings derived from large (*g*) and small (*s*) seeds in relation to sowing density and depth (0.5 and 3.0 cm) in *Spergula vernalis*

100% – total number of seedlings. Number of seeds sown per 100 cm^2: dotted line – 100, broken line – 200, continuous line – 400

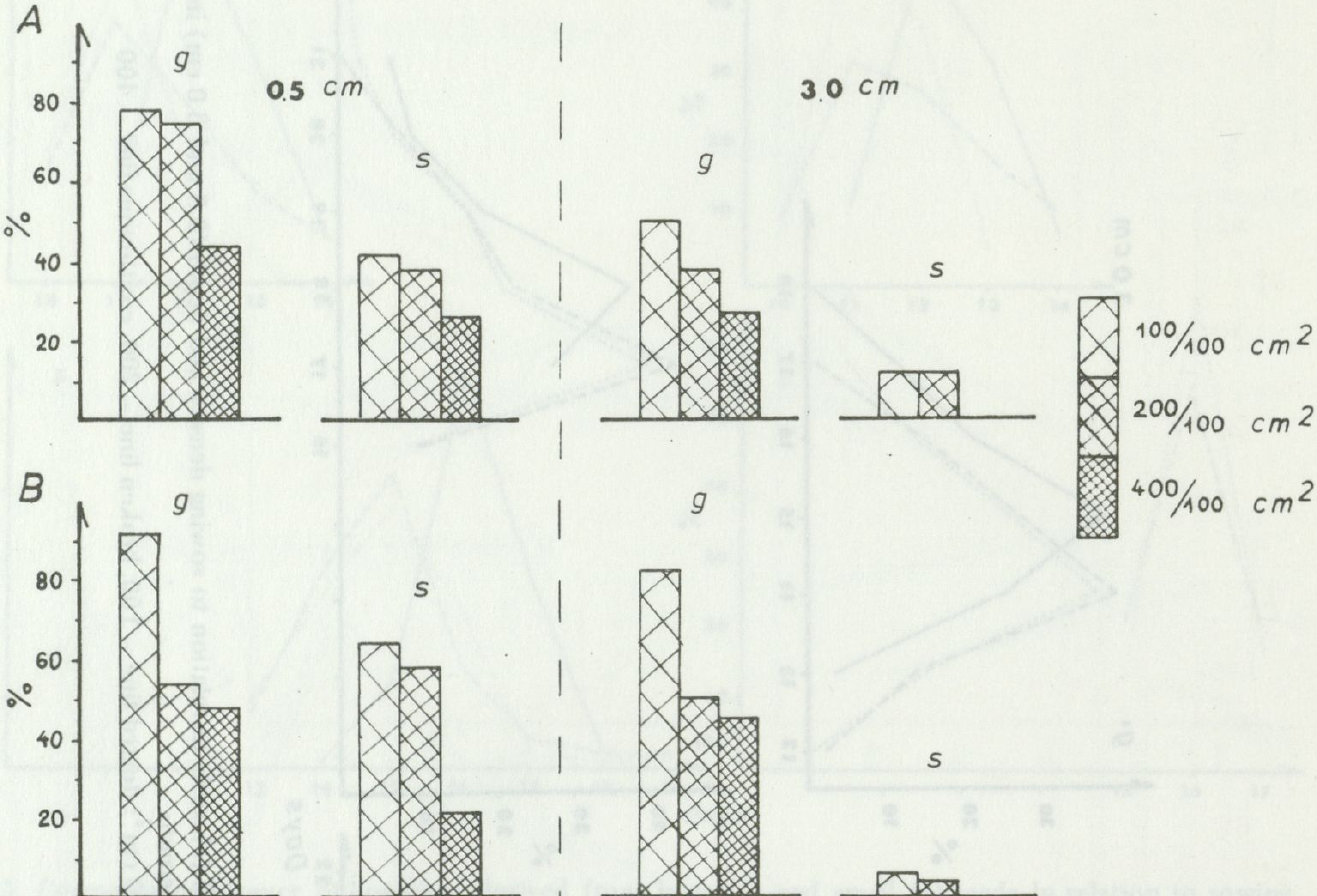

Fig. 5. Per cent emergence of seedlings relative to the number of seeds sown (*A*) and percentage of seedling survivors relative to total number of seedlings (*B*) with different seed sizes and sowing densities and depths (0.5 and 3.0 cm) in *Androsace septentrionalis*
g – large seeds, *s* – small seeds

The per cent mortality of seedlings relative to the number of seedlings, which emerged on the individual days, showed a close relationship to the emergence time only at high seed densities. At lower densities no such direct relationship could be seen, although the per cent survival of seedlings that appeared at an earlier time was always higher than that of those seedlings which had emerged the latest (Fig. 9). This finding applies to both sowing depths.

In Table I the sizes of seedlings are compared. The unit of comparison in this summary is the average size of the above-ground and underground parts of the seedlings of each of the species, derived from large seeds at low density and shallow sowing. As no effect was found of the depth of sowing on the ultimate size of the seedlings, in Table I data have only been given, as an example, for a shallow sowing.

An analysis of the data contained in Table I shows that the factor determining the size of the seedlings was the size of the seeds. The density of the seeds sown appears to have had no significant effect.

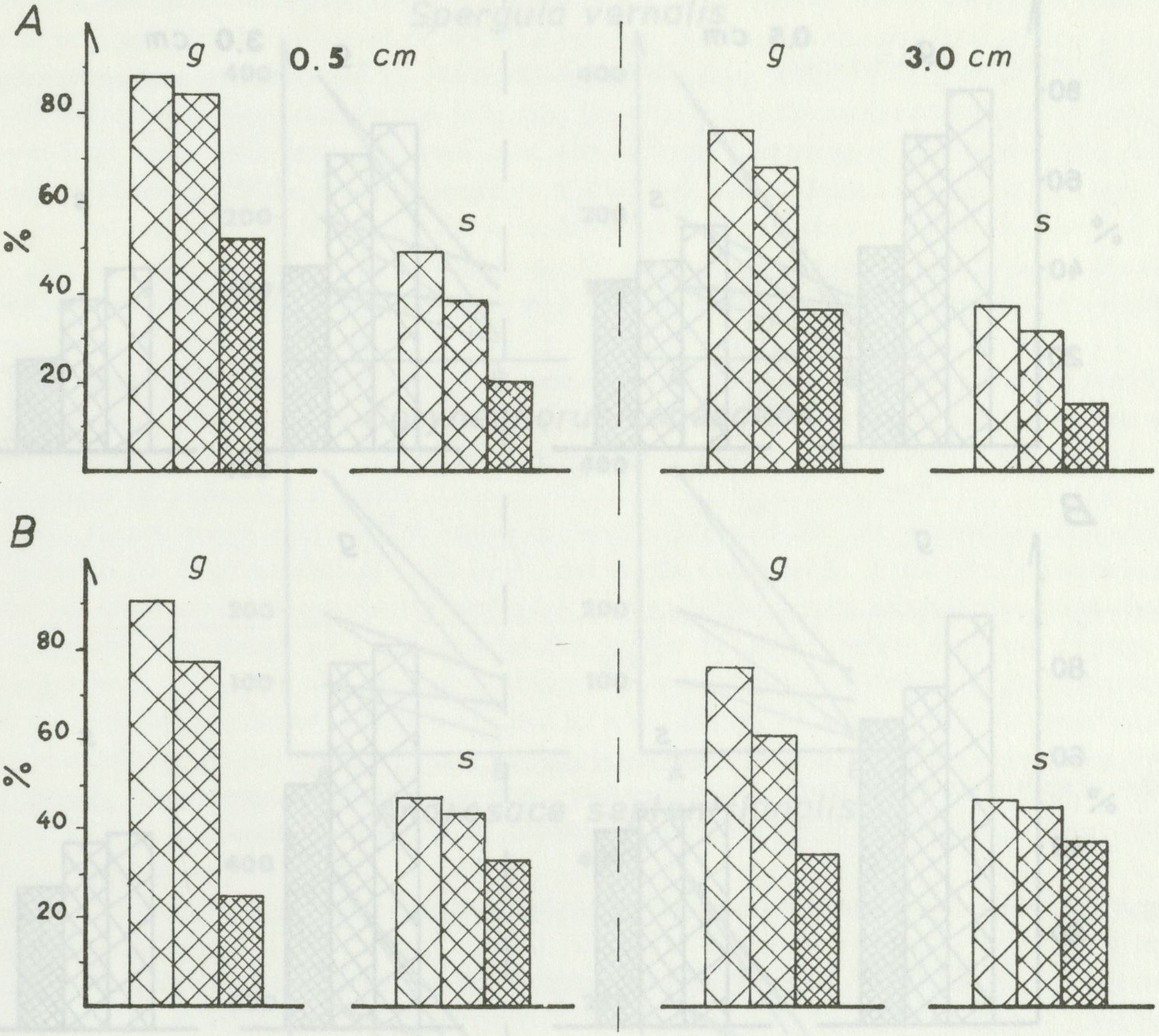

Fig. 6. Per cent emergence of seedlings relative to the number of seeds sown (A) and percentage of seedling survivors relative to total number of seedlings (B), with different seed sizes and sowing densities (see Figure 5) and depths (0.5 and 3.0 cm) in *Spergula vernalis*

g – large seeds, *s* – small seeds

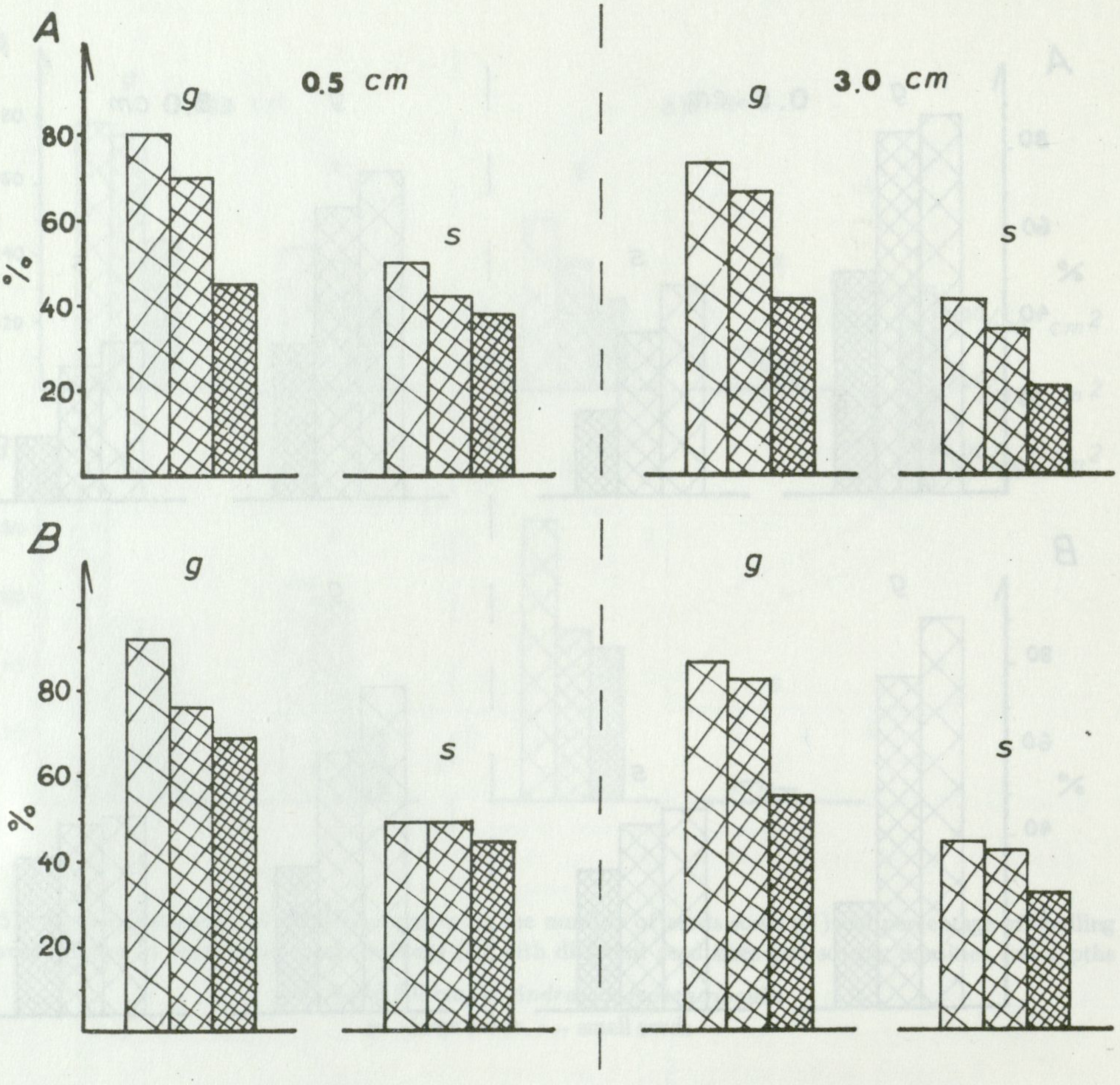

Fig. 7. Per cent emergence of seedlings relative to the number of seeds sown (A) and percentage of seedling survivors relative to total number of seedlings (B), with different seed sizes and sowing densities (see Figure 5) and depths (0.5 and 3.0 cm) in *Corynephorus canescens*
g – large seeds, *s* – small seeds

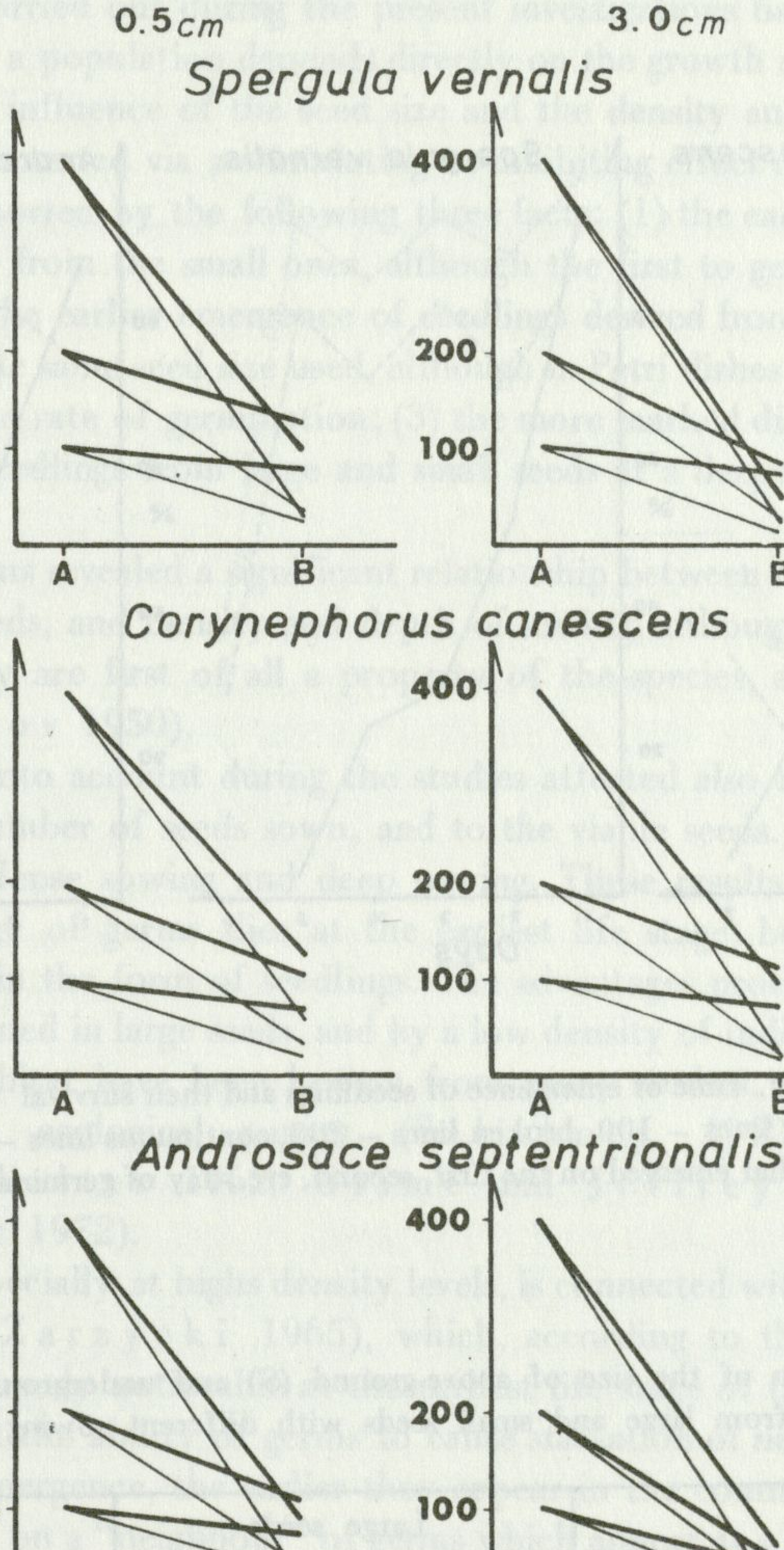

Fig. 8. Effect of seed density (*A*) on the number of survivors (*B*) at shallow (left side) and deep (right side) sowing

Thick line – seedlings from large seeds, thin line – seedlings from small seeds

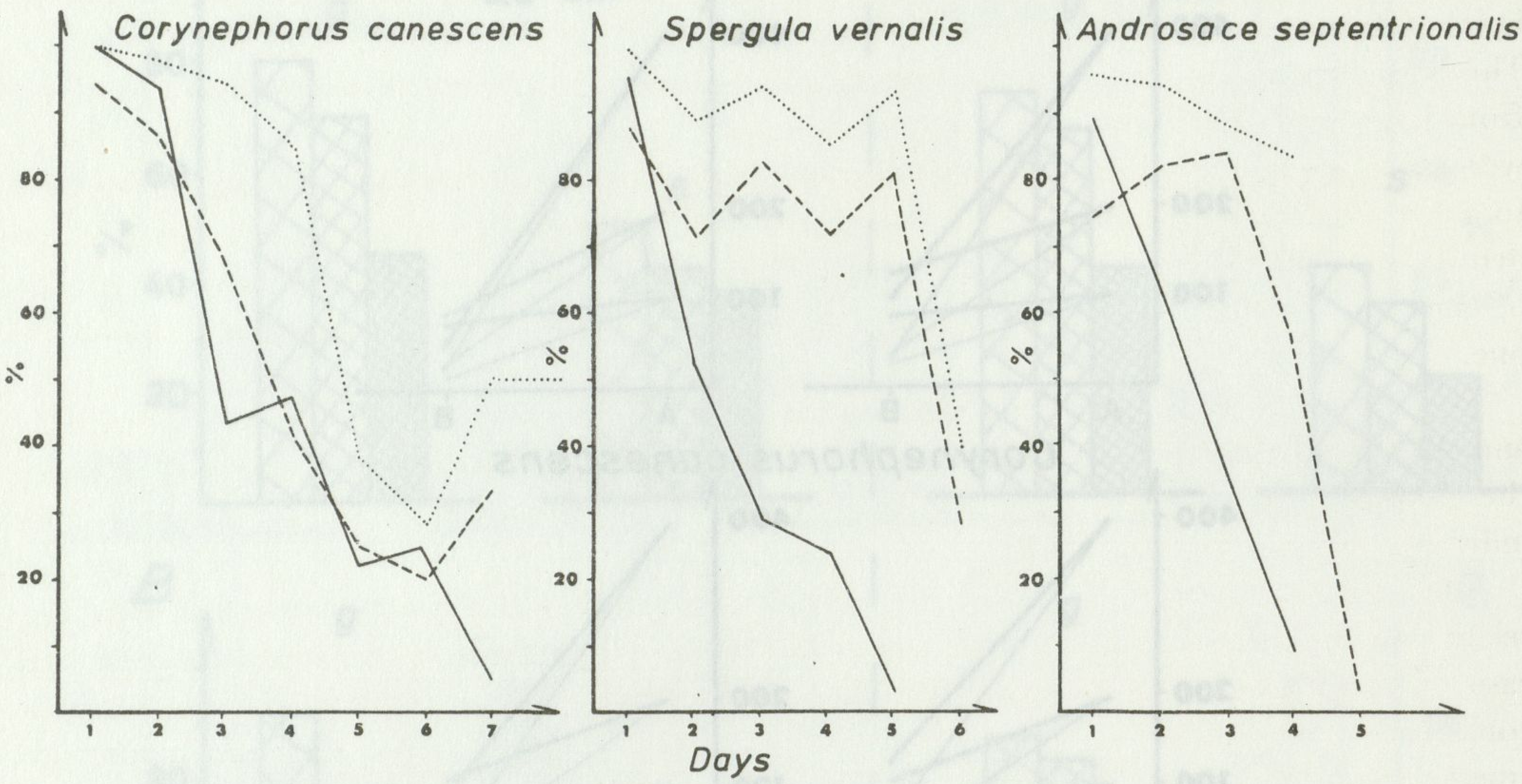

Fig. 9. Time of emergence of seedlings and their survival
Number of seeds sown: dotted lines – 100, broken lines – 200, continuous lines – 400. 100% – number of seedlings that emerged on the first, second, etc., day of germination

Table I. Comparison of the size of above-ground (S) and underground (R) parts of seedlings derived from large and small seeds with different sowing densities used

Species		Large seeds			Small seeds		
		number of seeds sown per 100 cm^2					
		100	200	400	100	200	400
Corynephorus canescens	*S*	1	0.99	0.91	0.89	0.89	0.87
	R	1	1.02	0.89	0.85	0.86	0.81
Spergula vernalis	*S*	1	1.01	0.93	0.79	0.78	0.71
	R	1	0.98	0.96	0.72	0.73	0.79
Androsace septentrionalis	*S*	1	0.97	0.90	0.76	0.72	0.69
	R	1	0.97	0.91	0.78	0.74	0.71

4. DISCUSSION

The experiments carried out during the present investigations have shown that the time of seedling emergence in a population depends directly on the growth rate of the germs. Although it is indisputable, the influence of the seed size and the density and depth of sowing is of an indirect nature, being exerted via a stimulating or inhibiting effect on the growth of the germs. This statement is supported by the following three facts: (1) the earlier emergence of seedlings from large seeds than from the small ones, although the first to germinate in the Petri dishes were small seeds; (2) the earlier emergence of seedlings derived from a thin sowing, as opposed to a dense one, with the same seed size used, although in Petri dishes no effect was found of the density of seeds on the rate of germination; (3) the more marked differences between the time of emergence of the seedlings from large and small seeds at a deeper sowing than at a shallow one.

The studies have thus revealed a significant relationship between the growth rate of seedlings and the size of the seeds, and density and depth of sowing, although both the growth rate and the germinating energy are first of all a property of the species, and even a property of the individual (Rabotnov 1950).

The factors taken into account during the studies affected also the percentage of seedlings relative to the total number of seeds sown, and to the viable seeds. It was clearly lower in the case of small seeds, dense sowing and deep sowing. These results support the point that a considerable percentage of germs dies at the earliest life stage, before they can manage to emerge from the soil in the form of seedlings. The advantages provided by larger amounts of stored materials contained in large seeds, and by a low density of individuals with a poor supply of nutrients in the habitat have been known from many studies, and have been many times discussed in various ecological papers (Salisbury 1942, Rabotnov 1950, Sukačev 1953, Walter 1962, Grime and Jeffrey 1965, Harper 1967, Ross and Harper 1972).

Germ mortality, especially at highs density levels, is connected with the competitive struggle for space and food (Zarzycki 1965), which, according to the paper by Ross and Harper (1972) is already noticeable at the earliest life stage of the germs. The two authors are of the opinion that the ability of germs to cause starvation of neighbouring germs depends on the time of their emergence, the earlier they appear in the common area, the stronger this ability is; the influence on a "neighbour" of germs which appear at a later time is much weaker.

It is known also from studies carried out so far tnat the competition among germs causes a reduction in their numbers, or in the size or weight of the seedlings that will develop from them, in the latter case the number of germs remaining the same (Harper and McNaughton 1962, Yoda 1963 – after Harper 1967, Antonovics 1972).

In the case of the species studied during the present series, at high seed densities there occurred primarily a reduction in the number of germs, due to which the numbers of seedlings recorded at the end of the experiments were very similar. The numbers of seedlings, equalized to a considerable extent in spite of the great differences in the density of the seeds sown, confirmed the view held by Yoda (1963 – after Harper 1967) that regardless of the differences between the initial populations, the maximal population densities tend to converge as time passes.

Due to the fact that at high densities there occurred a considerable reduction in the number of germs and seedlings, the size of the seedlings did not vary significantly with the different sowing densities used. Because it was impossible to culture seedlings at very high densities, it would be difficult to speak about any possible relationships between the density of sowing and the seedling size or weight. This relationship is known to be common in many plant species (Witt 1961, Obeid 1965, Palmblad 1968, Marschall and Jain 1969, Putwain and Harper 1970, Wilkoń-Michalska 1976).

The positive effect, found in the present study, of the larger size of the seeds on the size of the seedlings seems to be only indirect. It results mainly from the faster rate of growth of the germs, owing to which the seedlings are able to occupy a larger biological space, and thereby obtain better conditions for their growth.

When discussing the results of the present investigations, the fact should also be noted that both the time of germination and the process of germination, as well as the emergence of seedlings are to a large degree determined genetically, thus being to some extent independent of the external conditions. This is indicated by the fairly large time amplitude between the appearance of the first seedling and of the last seedling, and between the germination of the first seed and of the last one, in spite of the fact that the conditions which accompanied the germination and the growth of seedlings were identical.

An analysis of the per cent mortality of seedlings in relation to an earlier or later emergence also leads to the conclusion that the viability of the seedlings, too, is to some extent an individual character. A steady increase in the percentage of seedlings dying as they appeared in the plots could only be seen at the highest density. This was similar to the situation observed under field conditions (Symonides 1977). At lower densities the relationship between the mortality of seedlings and the time of their emergence did not occur so consistently in any of the species studied. The differences in the picture of this relationship between field conditions and a pot culture are certainly connected with the period of germination and the period needed by the seedlings to get fixed, because in pot culture these periods are much shorter. This in turn reduces the differences in the size of the individual seedlings and their development, and thereby also differences in the competitive power among the seedlings emerging successively. For example, the period of germination of *Corynephorus canescens* seeds in a natural habitat is three, or even four times as long as under laboratory conditions. It is obvious that with a large time amplitude the first seedlings will be much larger and will have a greater ability to exert an influence on those seedlings which emerge in a later period. Such a situation does not occur in a pot culture if the differences in the time of emergence of the seedlings are not so great.

5. CONCLUSIONS

On the basis of the present studies the following conclusions can be put forward:

1. Seed size and the density and depth of sowing determine first of all the rate of growth of the germs, which in turn affects the time and rate of growth of the seedlings.
2. The number of seedlings is smaller not only in relation to the number of seeds sown, but also relative to the number of germs. This indicates germ mortality at the earliest stage of their life.
3. The per cent mortality of germs and seedlings depends on the size of seeds, as well as on the density and depth of sowing.
4. Regardless of the number of seeds sown (within the sowing density range used in the experiments), the species under study showed a strong tendency to even the numbers of seedling survivors.

5. Due to a high mortality of germs and seedlings, the factors taken into account during the studies, except the seed size, did not significantly affect the size of the seedling survivors.

6. The less marked relationship between the survival of seeds and the time of their emergence, as compared with the close relationship observed under field conditions, probably resulted from the fact that in the pot culture the time of seed germination and the time needed by the seedlings to get fixed were shorter.

6. SUMMARY

Laboratory experiments were carried out, the aim of which was to establish a possible influence of the size of seeds, and of the density and depth of sowing on the time and course of germinating, and fixing of the seedlings, and on the survival of seedlings in three psammophyte species: *Corynephorus canescens, Spergula vernalis* and *Androsace septentrionalis.* The studies were carried out in continuation of earlier observations of seedling mortality in psammophyte populations under natural conditions (Symonides 1977).

The germinating capacity of large and small seeds (selected by means of a series of sieves differing in mesh size – in the case of seeds of *Spergula vernalis* and *Androsace septentrionalis,* and by direct measurement – in the case of *Corynephorus canescens* caryopses) at two different sowing densities (100 and 300 seeds) was assessed in Petri dishes. In the soil experiments, large and small seeds of each species, three different sowing densities (100, 200 and 400 seeds per 100 cm^2), and two different sowing depths (0.5 and 3.0 cm) were used. Each experimental variant was replicated three times. At the end of the experiments the seedlings were removed from the soil, whereafter their underground and above-ground parts were measured. The calculations made concerned the percentage of germs and seedlings, relative to the total number of seeds sown, percentage of seedlings relative to the number of germs, and the per cent mortality of seedlings, depending on the varying time of their emergence – separately for each variant of seed size, and density and depth of sowing. The effect was analyzed of the above-enumerated factors on the germination, survival and on the size of the seedling survivors.

Small seeds were found to germinate earlier, but in a smaller percentage than the large seeds, the density of the seeds sown having no significant effect on the rate and course of germination (Fig. 1). Under soil conditions, seedlings derived from large seeds, and thin and shallow sowing emerged faster (Figs. 2–4), and a larger percentage of them survived than of those derived from small seeds, at dense and deep sowing (Figs. 5–7). Regardless of the number of seeds sown, the numbers of seedlings which survived until the end of the experiments were fairly similar (Fig. 8). Because the number of seedlings which emerged at a high density had been reduced considerably, no effect of density on the size of seedling survivors could be seen (Table I); this relationship occurs in many plant species (Witt 1961, Palmblad 1968, Marschall and Jain 1969, Putwain and Harper 1970, Wilkoń-Michalska 1976).

A comparison of the results from the experiments carried out in Petri dishes with those obtained from pot culture leads to the conclusion that the effect of the factors, taken into account during the investigations, on the time and rate of emergence of the seedlings is only of an indirect nature, because it is exerted via their influecence on the rate of growth of the germs. A smaller number of seedlings, relative to the number of seeds sown and to the number of germs, indicates a strong competition among the germs for space and food, the competition being particularly evident when there is a high density pressure (Salisbury 1942, Rabotnov 1950, Sukačev 1953, Walter 1962, Grime and Jeffrey 1965, Harper 1967, Ross and Harper 1972).

7. POLISH SUMMARY

Przeprowadzono doświadczenia w warunkach laboratoryjnych, których celem było ustalenie ewentualnego wpływu rozmiaru nasion, gęstości i głębokości siewu na termin i przebieg kiełkowania i utwierdzania siewek oraz na przeżywanie siewek u trzech gatunków psammofilnych: *Corynephorus canescens, Spergula vernalis* i *Androsace septentrionalis.* Badania te były kontynuacją wcześniej przeprowadzonych obserwacji nad wymieraniem siewek w populacjach psammofitów w warunkach naturalnych (Symonides 1977).

Zdolność kiełkowania dużych i małych nasion (wyselekcjonowanych za pomocą systemu sit o różnej średnicy oczek w przypadku nasion *Spergula vernalis* i *Androsace septentrionalis* oraz metodą bezpośredniego pomiaru w przypadku ziarniaków *Corynephorus canescens*) w dwóch gęstościach siewu (100 i 300 sztuk) oceniono na płytkach Petriego. Doświadczenia glebowe uwzględniały duże i małe nasiona każdego gatunku, trzy gęstości siewu (100, 200 i 400 nasion na powierzchni 100 cm^2) oraz dwie głębokości siewu (0,5 i 3,0 cm). Każdy wariant powtórzony był trzykrotnie. Przy końcu doświadczenia siewki usunięto z gleby oraz zmierzono ich części podziemne i nadziemne. Obliczenia dotyczyły procentu kiełkowania i wyrastania siewek w stosunku do ogólnej liczby wysianych nasion, procentu wyrosłych siewek w stosunku do liczby kiełków oraz procentu wymierania siewek w związku z różnym terminem ich wyrastania – oddzielnie dla każdego wariantu rozmiaru nasion, gęstości i głębokości siewu. Przeprowadzono analizę wpływu wymienionych czynników na kiełkowanie, przeżywanie i rozmiar przeżywających siewek.

Okazało się, że nasiona małe kiełkują szybciej, ale w mniejszym procencie niż duże, przy czym zagęszczenie posianych nasion nie wpływa istotnie na tempo i przebieg kiełkowania (rys. 1). W warunkach glebowych szybciej wyrastały siewki pochodzące z dużych nasion, rzadkiego i płytkiego siewu (rys. 2–4) i w wyższym procencie przeżywały niż pochodzące z nasion małych, przy gęstym i głębokim siewie (rys. 5–7). Niezależnie od liczby posianych nasion stwierdzono w znacznym stopniu wyrównanie liczby przeżywających do końca doświadczeń siewek (rys. 8). Wskutek znacznej redukcji liczby siewek wyrosłych w dużym zagęszczeniu – nie stwierdzono wpływu zagęszczenia na rozmiar przeżywających siewek (tab. I); zależność ta występuje u wielu gatunków roślin (Witt 1961, Palmblad 1968, Marschall i Jain 1969, Putwain i Harper 1970, Wilkoń-Michalska 1976).

Porównanie wyników doświadczeń przeprowadzonych na szalkach Petriego z wynikami hodowli w warunkach glebowych prowadzi do wniosku, że wpływ uwzględnionych w badaniach czynników na termin i tempo wyrastania siewek jest tylko pośredni, realizuje się bowiem poprzez oddziaływanie na tempo wzrostu kiełków. Niższa liczba wyrosłych siewek, w porównaniu z liczbą wysianych i wykiełkowanych nasion, świadczy o silnej konkurencji między kiełkami o przestrzeń i pokarm, zaznaczającej się szczególnie wyraźnie przy dużej presji zagęszczenia (Salisbury 1942, Rabotnov 1950, Sukačev 1953, Walter 1962, Grime i Jeffrey 1965, Ross i Harper 1972).

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