EFFECT OF SEED MASS ON GERMINATION AND GROWTH IN THREE DOMINANT SPECIES IN SOUTHERN BRAZILIAN COASTAL DUNES

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(With 1 figure)

ABSTRACT

The effect of seed mass on germination and growth was tested in fresh-seeds of *Blutaparon portulacoides*, *Panicum racemosum*, and *Spartina ciliata*, selected at random in southern Brazilian populations. The seed mass varied within a population of the three species. Both *B. portulacoides* and *P. racemosum* showed normal frequency distribution of seed mass, while *S. ciliata* did not. Significant differences were observed in seed germination between large and small seeds of all species. In all species the capacity of seedling elongation was greater in seedlings of large seeds than those of small ones. Relative growth rate of seedlings of *P. racemosum* and *S. ciliata* decreased with time in all seed mass size-classes. On the other hand, the relative growth rate of *B. portulacoides* seedlings increased during the first 40 days. Seed mass is an important biological factor, affecting seed germination, seedling elongation, and growth of these species, and favoring large seeds, specially in areas of active sand accretion like coastal dunes.

Key words: germination, seedling growth, *Panicum racemosum*, *Spartina ciliata*, *Blutaparon portulacoides*.

RESUMO

Efeito da massa das sementes na germinação e no crescimento em três espécies dominantes das dunas costeiras do sul do Brasil

O efeito da massa das sementes sobre a germinação e o crescimento foi testado com sementes de *Blutaparon portulacoides, Panicum racemosum* e *Spartina ciliata* coletadas aleatoriamente em populações no sul do Brasil. A massa das sementes variou dentro das populações das três espécies. Ambas, *B. portulacoides* e *P. racemosum*, mostraram distribuição normal na freqüência no peso das sementes, enquanto *S. ciliata* não apresentou distribuição normal. Diferenças significativas foram observadas na germinação das sementes entre sementes grandes e pequenas nas três espécies. A capacidade de alongamento das plântulas das três espécies é maior nas plântulas originadas de sementes grandes do que nas provenientes de sementes pequenas. As taxas de crescimento relativo das plântulas de *P. racemosum* e *S. ciliata* diminuíram com o tempo em todas as classes de massa de sementes. Por outro lado, a taxa de crescimento relativo das plântulas de *B. portulacoides* aumentou ao longo dos primeiros 40 dias. A massa das sementes é um importante fator biológico, porque afeta a germinação, o alongamento das plântulas e o crescimento nas espécies, favorecendo assim as sementes maiores, especialmente em áreas de ativa deposição de areias, como as dunas costeiras.

Palavras-chave: germinação, crescimento das plântulas, *Panicum racemosum*, *Spartina ciliata*, *Blutaparon portulacoides.*

INTRODUCTION

Seed size (usually measured as mass) has long been regarded as an important aspect of plant reproductive biology. Traditionally, seed mass within a plant species is considered a remarkably constant characteristic (Harper *et al*., 1970; Silvertown, 1981). However, other studies have demonstrated that seed mass within a species or even an individual plant can vary greatly (Harper *et al*., 1970; Schaal, 1980). Salisbury (1942) recognized that although seed mass varied between species, seed size was correlated with habitat and tended to increase with successional maturity of the community.

Differential seed size may have several important ecological implications. Variation in seed mass within a species may affect seed germination (Schaal, 1980; Weis, 1982) and germination rate (Weis, 1982; Zhang & Maun, 1990). Large seeds frequently have greater percent germination or emergence than small seeds (Weis, 1982; Hendrix, 1984). On the other hand, small seeds may germinate more quickly than large seeds and, thus, have a competitive advantage (Howell, 1981). Seed size also affects seedling biomass (Zimmerman & Weis, 1983): usually, the seedlings from large seeds are larger than those from small seeds, especially in the early stages of growth (Schaal, 1980; Saverimuttu & Westoby, 1996). The initial seedling size differences may persist until maturity (Schaal, 1980; Weis, 1982) or become imperceptible with time (Zimmerman & Weis, 1983) because of the differential relative growth rate among seedlings from differently sized seeds (Lewis & Garcia, 1979; Zhang & Maun, 1990). Some studies (Zimmerman & Weis, 1983) indicate that a higher relative growth rate of seedlings from small seeds exists only in the early stages of development, and/or that the RGR may be reduced in competitive conditions (Westoby *et al.*, 1996).

The aim of this study was to (a) investigate the variation in seed size in natural populations of *Panicum racemosum* (Beauv.) Spreng., *Spartina ciliata* Brong, and *Blutaparon portulacoides* (St.-Hil.) Mears from southern Brazilian coastal dunes; (b) determine the differences in germination and elongation of different-sized seeds of the three species; and (c) examine the effect of seed mass on seedling growth.

MATERIAL AND METHODS

Seed mass variation

Seed size obviously refers directly to seed volume. However, because seed shapes are so varied, volume is often difficult to measure, and mass is commonly used as a size index (Wilson, 1983).

The mass of 590, 580, and 665 freshseeds of *Panicum racemosum*, *Spartina ciliata* and *Blutaparon portulacoides* respectively, selected at random in southern Brazilian populations (32°27'S; 52°21'W) were recorded with an electronic balance. The cumulative means of seed mass in the samples were calculated as increased. When the sample size exceeded 300, 450, and 525 seeds of *Panicum*, *Spartina*, and *Blutaparon*, respectively, the mean seed mass and the variance remained fairly constant, and it was thus assumed that the samples reflected the true variation in the seed population for all three species. The distributions of individual seed masses for each species were tested for normality (Kolmogorov-Smirnov test; Zar, 1984).

Effect of seed mass on germination

One hundred seeds from each size class (large, medium, and small) of each species were weighed and individual seeds kept separately in four replicate plastic boxes, each with 25 compartments (1 x 1 cm). It was therefore possible to correlate their size with time and total germination. The three size classes were chosen to avoid overlapping of in their seed masses.

The twenty-five seeds per box were soaked in 2 ml of distilled water per compartment of each plastic box, on two layers of filter paper (Whatman N. 1). The plastic boxes were placed randomly in an incubator maintained at alternating temperatures with 12 hours of ilumination at 30°C and 12 hours of darkness at 15°C. Previous studies showed that these germination conditions were the best for the three species (Cordazzo, 1994). Germinated seeds were counted every day and removed. At the end of the experiment, all ungerminated seeds were examined for viability with the tetrazolium test. Germination percentage and germination rate (GR) in each size class were recorded and transformed to arcsin square root values before analysis of data using a ONE-WAY analysis of variance (ANOVA).

Tukey's multiple range test was used when the ANOVA showed a significant difference (Zar, 1984). However, the data shown in the tables have not been transformed. The germination rate was calculated according to Mugnisjah & Nakamura (1986) and can be expressed as follows:

$$GR = 100/\sum Ni \times \sum (Ni/Ti)$$

where Ti is the day after germination beginning and Ni, the number of seeds germinating on day Ti. We also observed, a *time lag* (time in days between the beginning of the experiment and that of germination). Together, lag time, germination rate, and final germination proportion are considered an adequate indication of germination performance for most species (Shipley & Parent, 1991).

Effect of seed mass on seedling growth

One-hundred 5-day old seedlings were selected from each size class of seed mass and eighty were planted individually in 9 cm plastic pots filled with 4:1 sand and John Innes compost N. 2 mixture. The pots were then placed randomly on a bench in an environmental cabinet kept at 25°C day (14 hours) and 15°C (10 hours) night temperatures. Each 10 days after planting, twenty plants from each size class were harvested and gently washed. The dry masses of leaves and roots were measured after 48 hours in an oven at 80°C. There were four successive harvests. Twenty 5-day old seedlings from each size class were dried, measured, and used as the initial seedling biomass of each size class. Measurements were transformed to natural logarithms for normalization prior to variance analysis. Relative growth rate (RGR) was then calculated according to the equation;

$$RGR = (\ln W2 - \ln W1)/t2 - t1$$

where t is the time in days and W1 and W2 are the dry masses per plant in milligrams at t1 and t2, respectively (Hunt, 1990).

RESULTS

Seed mass variation

The seed mass of *Panicum racemosum* varied within the population by a factor of about four, from 3.2 to 12.4 mg per seed. The mean seed mass of this population was 7.9 ± 0.08 mg (mean ± standart error), which was lower than the mode (8.9 mg). The frequency distribution of seed mass was normal (D-statistic 0.0602).

Seed mass of *Spartina ciliata* varied greatly, from 0.1 to 5.6 mg, with a mean of 2.4 ± 0.03 mg. which was equal to the mode. The seed mass distribution was non-normal (D-statistic 0.0535), skewed to the right (g1 = 0.085), and platykurtic (g2 = –0.295).

The mean mass of the field population of *Blutaparon portulacoides* seeds was 0.9 ± 0.01 mg and seed mass ranged from 0.1 to 1.8 mg with a modal class of 0.8 mg, lower than the mean. The seed mass distribution was normal (D-statistic 0.0582).

Effect of seed mass on germination

The total germination percentage of *Panicum racemosum* for small seeds (less than 6.8 mg) was 16%, and increased significantly to 30.4% and 31.2% for medium and large seeds, respectively (Table 1). The germination rate of seeds in the three classes showed a significant difference only in relation to small versus medium and large seeds (Table 1). Similarly, the lag time was different from medium and large seeds (4 days) to that of the small ones (7 days) (Table 1).

The total germination was significantly different (large > medium > small) among the different seed-size classes in *Spartina ciliata* (Table 1). However, the rate of seed germination in different sizes was not significantly different (Table 1). The lag time for large and medium seeds was 2 days and 4 days for small ones (Table 1).

The percentage of *Blutaparon portulacoides* seeds germinating at various times are shown in Table 1. Analysis of the data showed significant differences in total germination of large and medium seeds in relation to small seeds. The rate of germination showed similar differences. The lag time of large seeds (1 day) was different for medium and small seeds (2 days) (Table 1).

Seed mass effect on seedling growth

The effect of seed mass on seedling growth of *Panicum racemosum* during the 40 days after germination are represented in Fig. 1A. Large seeds produced heavier seedlings than the smaller ones did. However, the differences in seedling mass were significant only between 20 and 30 days. Thereafter, the differences disappeared completely.

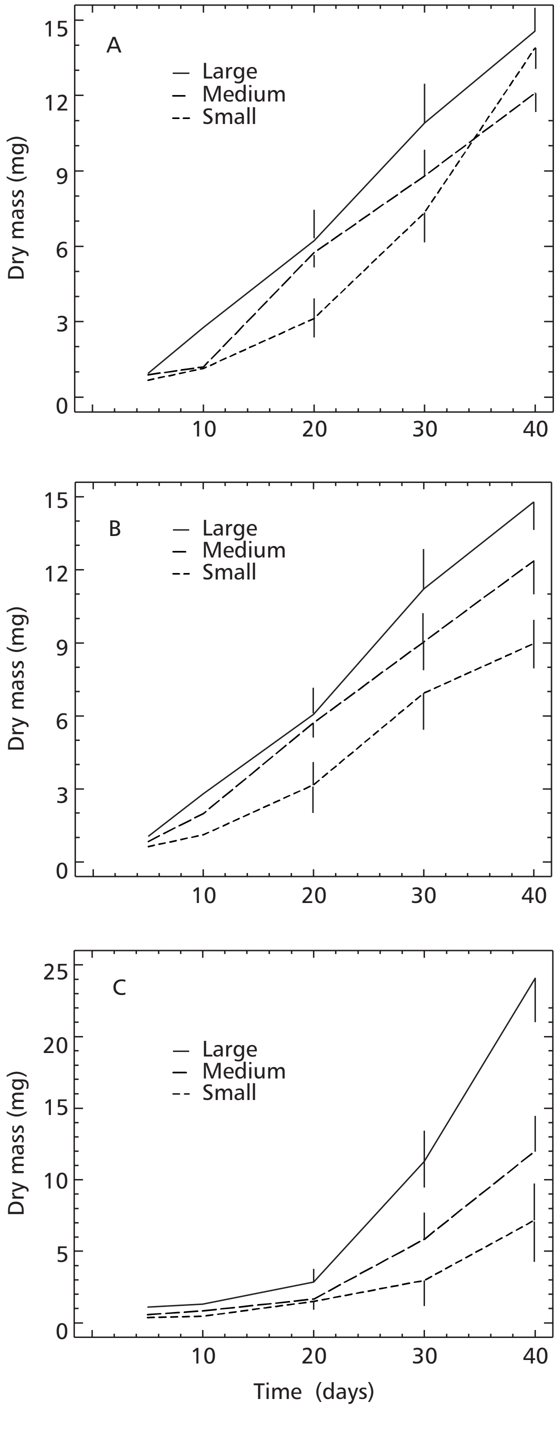

Fig. 1 — Seedling growth (mean ± SE) expressed as dry mass (mg) over 40 days from three different seed-size classes (seed mass) in (A) *Panicum racemosum*, (B) *Spartina ciliata*, and (C) *Blutaparon portulacoides*.

TABLE 1

Lag time (L), mean ± SE of germination (G%) and rate of germination (RG) of *P. racemosum, S. ciliata,* and *B. portulacoides* in three different-sized classes of seeds (expressed as seed mass) from a population of southern Brazilian coastal dunes.

Size (mg)	L (days)	G%	RG
Panicum racemosum			
Large (10.3 ± 0.6)	4	31.2 ± 0.7 (a)	22.1 ± 0.7 (a)
Medium (8.4 ± 0.6)	4	30.4 ± 0.8 (a)	21.5 ± 1.2 (a)
Small (5.7 ± 0.7)	7	16.6 ± 0.8 (b)	11.1 ± 1.3 (b)
Spartina ciliata			
Large (3.5 ± 0.18)	2	98.0 ± 0.2 (a)	16.9 ± 0.5 (a)
Medium (2.5 ± 0.11)	2	88.2 ± 1.3 (b)	16.8 ± 0.4 (a)
Small (1.3 ± 0.03)	4	75.1 ± 1.7 (c)	17.0 ± 0.7 (a)
Blutaparon portulacoides			
Large (1.2 ± 0.01)	1	72.0 ± 0.4 (a)	33.5 ± 3.3 (a)
Medium (0.7 ± 0.02)	2	65.2 ± 2.5 (a)	33.7 ± 2.4 (a)
Small (0.3 ± 0.01)	2	32.0 ± 1.6 (b)	25.8 ± 0.6 (b)

Different letters in the same column indicate significant differences according to Tukey's multiple range test at 5% significance level.

The relative growth rate (RGR) decreased significantly over the 40 days after germination in seedlings from large seeds (Table 2). In seedlings from medium and small seeds, the relative growth rate increased significantly between 10 and 20 days (Table 2), but decreased significantly in seedlings from medium-sized seeds after 30 days (Table 2), while in seedlings from small seeds it was similar to the initial value. Significant differences were observed between seedlings from large and small seeds of *Spartina ciliata* harvested at 20, 30, and 40 days. The seedlings from medium-sized seed did not differ from the extremes (Fig. 1B). Similarly to *P. racemosum*, the relative growth rate of seedlings of *Spartina ciliata* from large seeds decreased significantly with time (Table 2). The seedlings from medium-sized and small seeds, however, increased in relative growth rate (RGR) at 20 days, but decreased again significantly after 30 days (Table 2). The dry mass for the three seed-size classes of *Blutaparon portulacoides* is represented in Fig. 1C. There were large differences in the dry matter accumulated in seedlings developed from large and small seed-size classes. After 40 days, the seedlings developed from the former were two to three times larger than those developed from medium and small seeds, respectively. The relative growth rate (RGR) increased with age increase of seedlings from large and medium seeds (Table 2) while remaining constant after 20 days in seedlings from small seeds (Table 2).

DISCUSSION

Seed size is one of the more stable morphological characteristics in many plant species (Harper *et al*., 1970; Silvertown, 1981). However, various studies have demonstrated that seed size within a species or even an individual plant can vary greatly (Schaal, 1980; Hendrix, 1984).

TABLE 2

Relative growth rate (g.g^{-1}.day^{-1}) of three different-sized classes (expressed as seed mass) of *P. racemosum, S. ciliata,* and *B. portulacoides* over 40 days after germination.

	Time (days)			
	0-10	**10-20**	**20-30**	**30-40**
Panicum				
Large	0.103 (a)	0.08 (b)	0.06 (c)	0.03 (d)
Medium	0.085 (a)	0.10 (b)	0.04 (c)	0.03 (c)
Small	0.052 (a)	0.09 (b)	0.09 (b)	0.06 (c)
Spartina				
Large	0.098 (a)	0.08 (a)	0.05 (b)	0.02 (c)
Medium	0.087 (a)	0.10 (a)	0.04 (b)	0.03 (b)
Small	0.055 (a)	0.10 (b)	0.08 (ab)	0.02 (c)
Blutaparon				
Large	0.016 (a)	0.05 (b)	0.09 (c)	0.11 (c)
Medium	0.015 (a)	0.04 (a)	0.08 (b)	0.09 (b)
Small	0.005 (a)	0.07 (b)	0.04 (b)	0.06 (b)

Different letters in the same row represent means statistically different according to Tukey's multiple range test at 5% significance level.

Several factors such as (a) competition between individual seeds for limited resources (Stanton, 1984), (b) microhabitat differences microhabitat (Keddy, 1982), (c) genetic control (Stanton, 1984), (d) plastic responses to environmental variation (Winn, 1988), and (e) trade-offs between seed size and seed number (e.g., *Panicum racemosum*, Cordazzo & Davy, 1994) may be responsible for this variation. Baker (1972) found a correlation between seed mass of individual seeds of nearly 2500 taxa over a range of environment conditions. He estimated a value of environmental 6.48 mg as mean seed mass for coastal strand and dunes, a value lower than the mean seed mass obtained from *Panicum racemosum*, but higher than that from *Spartina ciliata* and *Blutaparon portulacoides*.

Seed-size variation of a species may have ecological significance in a number of ways. The characteristic seed mass of a plant species probably represents a compromise between the requirements for dispersal and for establishment (Harper, 1977; Swanborough & Westoby, 1996). The need for wide dispersal would favor small-seed evolution (Fenner, 1983); the need for successful establishment creates a selection pressure for large seeds (Jurado & Westoby, 1992; Lloret *et al.*, 1999; Kidson & Westoby, 2000).

The germination experiments indicated that small seeds of *P. racemosum*, *S. ciliata*, and *B. portulacoides* have lower percent germination than larger seeds, suggesting a positive effect of seed mass on germination, which results from other species supports (Schaal, 1980; Zhang & Maun, 1990; Shaukat *et al.*, 1999; Kidson & Westoby, 2000). This behavior probably is an adaptation to establishment in areas with active sand burial, where the greater food reserves of large seeds may be an advantage.

The large-seed germination rate was significantly higher than that of small seeds, except for *Spartina ciliata*, which presented no differences in the three size classes. Results showing that large seeds of *Panicum racemosum* and *Blutaparon portulacoides* have higher germination rates than small ones do are in agreement with results on other species such as *Lupinus texensis* (Schaal, 1980), *Impatiens capensis* (Howell, 1981), *Mirabilis hirsuta* (Weis, 1982), *Xanthium strumarium* (Zimmerman & Weis, 1983), *Agropyron psammophilum* (Zhang & Maun, 1990), *Panicum virgatum* (Zhang & Maun, 1991), *Erica vagans* (Vera, 1997), and *Acacia nilotica* (Shaukat *et al*., 1999). Some studies by Stanton (1984), Zhang & Maun (1990), and Seiwa (2000) have suggested that early germinating seedlings have a higher competitive ability than later ones because they occupy the available space and preempt the limited resources. On the other hand, later-germinating seedlings can suffer increased mortality and/or reduced growth (Zimmerman & Weis, 1983). In the southern Brazilian sand-dune environment, the supply of nutrients is limited (Costa *et al*., 1991) and early germinating seedling probably have a better chance of growth and establishment at locations where seedling density is high, like depressions between dune ridges. The three species studied also showed that seedlings from large seeds present significantly higher elongation in darkness than do those from small seeds (Cordazzo, 1994). A small seed implies a small embryo with few food reserves. The seedling from a small seed is dependent from a very early phase in growth on its own independent assimilation. In contrast, the seedling from a large seed may have sufficient reserves to continue growth for a much longer period (Harper, 1977; Saverimuttu & Westoby, 1996). A high capacity for elongation of seedlings from large seeds would favor seedlings in areas of active sand accretion, as has been observed for other species (Howell, 1991; Maun, 1997).

It is generally agreed that large seeds tend to produce larger seedlings (Schaal, 1980; Weis, 1982; Zhang & Maun, 1990). Two patterns of absolute growth rate of the subsequent seedlings have shown that: (i) consistently greater absolute growth of seedlings from large seeds than from small seeds is maintained until maturity (Schaal, 1980; Stanton, 1984) and (ii) the initial size advantage of seedlings from large seeds may disappear with time because of higher relative growth rate of seedlings from small seeds (Lewis & Garcia, 1979). The results with seedlings of *Panicum racemosum* showed that the effect of seed mass was very important only for germination characters, but did not affect seedling dry mass after 40 days. However, seedlings from large seeds were significantly larger than those from small seeds at 20 and 30 days old. Some studies (Howell, 1981; Zimmerman & Weis, 1983) suggest that seedlings from small seeds have a higher relative growth rate (RGR) than those from large seeds. Thus, the initial size advantage of large seeds compared with small ones may be short-lived, e.g., seedlings of *P. racemosum*. Seedlings from large seeds showed a continual decrease in relative growth rate with time, although seedlings from small ones presented an increase in relative growth rate until they were 30-days old. Zhang & Maun (1990) found similar RGR values for *Agropyron psammophilum* but, in contrast, the decrease in relative growth rate of seedings from small seeds was greater than that of those from large ones.

There were significant advantages, maintained throughout, in dry matter accumulated in seedlings developed from large seeds of *Spartina ciliata* and *Blutaparon portulacoides* in relation to those developed from small ones. However, the relative growth rate (RGR) of seedlings from all seed-size classes fluctuated with time. For example, the RGR in *Spartina ciliata* seedlings decreased significantly from young plants to 40-day old ones in large seeds, but this reduction occurred at 30 days for seedlings from medium seeds and was different only at 20 days for seedlings from small seeds. Meanwhile, the seedlings of *Blutaparon portulacoides*, a pioneer species in the southern Brazilian coastal dunes, showed a relative growth-rate with time. However, the differences were significant only in seedlings from large-and-medium seeds. Grime (1979) has suggested that high RGR may be adaptive for colonizing species as it allows them to monopolize available space rapidly.

We conclude that the selective importance of fruit size in *Panicum racemosum* is potentially important only for germination of seeds and early growth of seedlings; seed mass effects on seedling growth disappear rapidly, at least under glasshouse conditions. On the other hand, the effects of seed mass were very important for the germination and growth of seedlings of *Spartina ciliata* and *Blutaparon portulacoides*, and could be of adaptive significance in establishing and maintaining the populations, because seedlings from large seeds are able to survive hazards (Westoby *et al*., 1996; Bonfil, 1998; Khurana & Singh, 2000) including coastal dunes stresses such as sand burial, drought, and few mineral nutrients. However, further studies are required to determine if this behavior and these characteristics are maintained in the field under conditions of intra- and inter-species competition.

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