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Seed mass, germination and seedling traits for some central Argentinian cacti

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Abstract

Seed size is one of the most important traits in the regenerative phase of a plant's life cycle; however, for cactus species the relationship of seed size and germination characteristics and seedling traits is still unclear. We studied the relationship between seed mass and germination and seedling characteristics in 17 cactus species from central Argentina, belonging to different genera and life forms. We measured seed mass, total seed germination, light requirements for germination and mean time to germination for these 17 cacti species; in addition, we recorded seedling size and shape in 15 species. To test light requirements we performed germination experiments under laboratory conditions at 25/15°C (day/night temperatures) and under light or dark conditions. We also calculated seedling volume by measuring seedling height and width. A shape index was obtained by dividing height by width (a value of 1 indicates 'globose' seedlings, whereas, as this value increases, seedlings become 'columnar'). We found no significant relationship between seed mass and any of the germination characteristics considered. However, species with heavier seeds produced bigger seedlings, which were more cylindrical. Adult growth was not totally determined by seedling 'growth form', because some species that had globose seedlings were columnar at the adult stage.

Keywords: Cactaceae, germination, seed mass, seedling traits, central Argentina

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Introduction

Cacti are important elements in the New World flora for many reasons. They are almost exclusively native to the Americas (Anderson, 2001), making an important contribution to species richness and endemisms in many regions (López, 2003; Ortega-Baes and Godínez-Alvarez, 2006; Giorgis *et al.*, 2011). The mountains of north-western Argentina and Bolivia are one of the three main areas of highest cactus diversity, together with Mexico and north-eastern Brazil (Ortega-Baes and Godínez-Alvarez, 2006). In central Argentina, the Córdoba Mountains are the southernmost portion of the mountains of north-western Argentina and Bolivia. However, few studies here have analysed basic aspects of cactus biology, such as regenerative traits (Gurvich *et al.*, 2008).

One of the most important topics in plant community ecology is the relationship among plant traits (Díaz *et al.*, 2004; Grime and Pierce, 2012). Seed mass has been indicated as one of the most important functional traits in plants (Lönnberg and Eriksson, 2013), being one of the principal traits influencing the early phases of a plant's life cycle (Fenner and Thompson, 2005). In addition, seed mass has been shown to be correlated with several seed or seedling traits, such as dispersal mode (Leishman *et al.*, 2000), seed moisture content (Sautu *et al.*, 2006), the capacity to form soil seed banks (Thompson *et al.*, 1993; Funes *et al.*, 1999), seedling size (Seiwa and Kikuzawa, 1996), and seedling relative growth rate (Shipley and Peters, 1990). However, the relationship between seed mass and germination attributes, such as total germination, response to light and time to germination, are still unclear, particularly in Cactaceae.

It has been proposed that seed mass may be related to seed germination percentage. However, studies considering this relationship have found different results. Some studies indicated a direct relationship (Galíndez *et al.*, 2009), others reported an inverse one

(Bu *et al.*, 2007; Wang *et al.*, 2009), whereas most studies found no relationship between seed mass and germination traits (Shipley and Parent, 1991; Morgan, 1998; Sautu *et al.*, 2006; Liu *et al.*, 2007). In Cactaceae, a study considering 54 species did not find a relationship between seed mass and total seed germination (Rojas Aréchiga *et al.*, 2012).

Germination response to light was proposed as one of the most important signals in a plant's life cycle (Pons, 2000). For example, it has been proposed that species forming persistent seed banks would be positively photoblastic in order to avoid germinating under the soil (Fenner and Thompson, 2005); moreover, pioneer tree species of tropical forests depend on an open gap to emerge (Baskin and Baskin, 1998). The effect of light on germination has been well studied in cactus species (Flores *et al.*, 2011). Species can be either light dependent (positively photoblastic) or show no light requirement for germination (Rojas-Aréchiga *et al.*, 1997; Rojas-Aréchiga and Vázquez-Yañes, 2000; Flores *et al.*, 2006); the latter phenomenon (negative photoblasticity) seems to be a non-existing response in cactus species (Guerrero *et al.*, 2011). In a study of 136 cactus species from different countries, Flores *et al.* (2011) found that seed mass was related to light dependence. They found that heavier-seeded species are more indifferent to light than lighter ones. However, Rojas-Aréchiga *et al.* (2012) found no relationship between seed mass and light dependence in 54 cactus species from the tribe Cacteae.

Time to germination is crucial for seed survival and seedling establishment. Norden *et al.* (2009) proposed that large-seeded species would have the fastest germination rate, since they are more likely to undergo high post-dispersal seed predation. In addition, small-seeded species that are generally highly persistent in the soil seed bank showed a delay in seed germination until proper germination conditions occur. Empirical data, however, are contradictory; for example, Norden *et al.* (2009) observed a positive relationship between time to germination and seed mass for tree tropical tree species, whereas Sautu *et al.* (2006) found no relationship. Cactus species generally germinate quickly (Álvarez-Aguirre and Montaña, 1997; Bárcenas-Argüello *et al.*, 2013). However, the relationship between time to visible germination and seed mass has been poorly analysed. In a study involving six columnar cactus species, Loza-Cornejo *et al.* (2008) found a positive relationship between seed mass and germination velocity.

The traits seedling size and shape might also be strongly dependent on seed mass. Heavier seeds may produce bigger seedlings, which in turn could affect their establishment (Moles and Leishman, 2008). In addition, seedling shape might be involved in the ability of the cactus to capture light or in dealing with temperature variations; therefore, this could be a key trait for seedling survival. To our knowledge, no previous study has analysed this relationship. Considering seedling characteristics, only Bowers and Pierson (2001) analysed the relationship between seedling traits and seed mass for North American cactus species. They compared seedling survival in two species with contrasting seed mass, *Carnegiea gigantea* and *Ferocactus wislizeni* with light and heavy seeds, respectively. They found that seed mass was positively related to seedling size and, therefore, to survival.

The Córdoba Mountains area is an important centre of cactus diversity in Argentina, both in the number of species (31) and in the presence of endemic ones (10) (Gurvich *et al.*, 2006; Giorgis *et al.*, 2011). However, different aspects of their biology, particularly reproductive biology, have not been fully addressed (Gurvich *et al.*, 2008). In the present study we investigated the relationship between seed mass and total germination percentage, response to light, mean time to germination, and seedling size and shape in 17 cactus species from mountain grasslands and xerophytic woodlands of central Argentina. Particularly, we hypothesized that seed mass will be positively related to total germination, mean germination time and seedling size. We also expect a negative relationship between seed mass and relative light germination (RLG).

Materials and methods

Study area and species selection

We studied 17 cactus species from the Cactoideae subfamily occurring in the north-western region of Córdoba province in central Argentina (see Table 1). Two main ecosystems are present in the study area, grasslands and xerophytic woodlands. Grasslands occur mainly above 1000 m asl, whereas below this altitude woodlands dominate the landscape (Giorgis *et al.*, 2011). We selected species based on their taxonomy, attempting to include species from all genera present in the area as well as globose and columnar ones, the two most common growth forms.

Experiments performed and variables measured

We collected mature fruits from at least ten individuals per species. Seeds were air-dried and stored in the laboratory at ambient conditions until the start of the experiments. We estimated seed mass by determining the weight of 50 dry seeds per species with a precision balance (0.1 mg). When seed mass was very low, we weighed a pool of ten seeds. We tested seed germination of the 17 species in a germination chamber under controlled light conditions (12/12 h daily photoperiod of about 38 $\mu mol\ m^{-2}\ s^{-1}$ cool white fluorescent light tubes). Darkness treatment consisted

Table 1. Growth form (C = columnar and G = globose), seed mass (mg), percentage of seed germination, relative light germination (RLG), mean germination time (MGT) and seedling height (mm) for cactus species from Córdoba (Argentina)

Species	Growth form	Seed mass (mg)	Germination (%)		RLG	MTG	Seedling height (mm)
			Light	Darkness			
Cereus hankeanus K. Schumann	C	1.60	67.77	28.89	0.70	13.15	6.32
Cleistocactus baumannii (Lemaire) Lemaire	C	0.51	85.56	10	0.89	9.94	2.7
Echinopsis aurea Britton & Rose	G	0.48	32.22	16.66	0.65	12.75	3.7
Echinopsis leucantha (Salm-Dyck) Walpers	C	0.74	68.67	0	1	15.51	3.07
Echinopsis candicans (Salm-Dyck) Hunt	C	0.25	45	14.16	0.76	13	–
Echinopsis spiniflora (K. Schumann) Berger	G	0.42	64.44	6.66	0.90	11.53	3.1
Gymnocalycium bruchii (Spegazzini) Hosseus	G	1.32	38	0	1	10.18	3.64
Gymnocalycium capillense (Schick) Hosseus	G	0.60	87.5	0.83	0.99	9.78	2.76
Gymnocalycium castellanosii Backeb.	G	0.19	93.33	0	1	11.54	2.69
Gymnocalycium monvillei (Lemaire) Britton & Rose	G	0.30	20.6	0	1	12.94	2.27
Gymnocalycium mostii (Gürke) Britton & Rose	G	0.08	60	0	1	9.69	1.96
Gymnocalycium quehlianum (F. Haage ex Quehl) Vaupel ex Hosseus	G	0.16	83.33	0	1	12.58	–
Gymnocalycium schickendantzii (F.A.C. Weber) Britton & Rose	G	0.40	51.11	2.22	0.95	18.44	2.52
Gymnocalycium stellatum Speg.	G	0.17	63.33	14.44	0.81	10.79	2.99
Harrisia pomanensis (F.A.C. Weber) Britton & Rose	C	1.95	53.34	0	1	15.38	5.65
Parodia mammulosa (Lemaire) Taylor	G	0.81	48.89	1.15	0.97	8.45	3.39
Stetsonia coryne (Salm-Dyck) Britton & Rose	C	0.34	88.33	0	1	13.09	2.86

of dishes wrapped in a layer of aluminium foil. All samples were exposed to a 12/12 h alternating temperature regime of 25/15°C. This temperature regime is optimal for germination of different species (including cacti) in the study area (Gurvich *et al.*, 2008; Funes *et al.*, 2009). We used three replicates per treatment. Each replicate consisted of 30 seeds placed on filter paper in 9-cm diameter Petri dishes and moistened with distilled water, for 30 d; for the species *Echinopsis candicans*, *Gymnocalycium capillense*, *G. mostii* and *Stetsonia coryne*, 40 seeds were used. We checked germination of seeds incubated in the darkness at the end of each experiment. Protrusion of the radicle was the criterion for seed germination.

For 15 species we also measured seedling size (i.e., height and width), shape and volume (Table 1). Seeds of those species were germinated in plastic pots in the greenhouse; 3 weeks after germination we measured seedling height and width of seven seedlings per species with a digital caliper. With these data we calculated a shape index (height/width ratio), with a value of 1 indicating spherical seedlings (typical of globose cacti) and a value departing from 1 indicating that seedlings become cylindrical (typical of columnar cacti). For spherical species, we calculated volume as: $(4\pi.r^3)/3$, where r is the radius. For cylindrical species, volume was calculated as: $\pi.r^2.h$, where h stands for height.

Data analysis

We calculated total percentage of seed germination, relative light germination (RLG; see Milberg *et al.*, 2000) and mean germination time (MGT; see Thapliyal and Phartyal, 2005). Since the dark treatment produced little or no germination (see Table 1), we estimated MGT only for seeds exposed to light. For RLG, we classified species as negatively photoblastic (RLG value 0–0.25), indifferent (0.25–0.75) and positively photoblastic (0.75–1). We analysed the relationship between seed mass and percentage of seed germination, RLG, MGT and the different measures of seedling size (height, width and volume) by calculating the Pearson correlation coefficient. Confidence intervals for the correlation coefficient were obtained by bootstrapping (Manly, 2006). We generated 9999 bootstrap samples. Correlation coefficients estimated after each bootstrap were used to obtain a frequency distribution. A correlation coefficient was considered significant if the bias-corrected and accelerated percentile interval (BCa) did not include zero (Moré *et al.*, 2012). We used the *boot* package (Canty and Ripley, 2011) of R software vs. 2.15.0 (R Development Core Team, 2012) to perform the bootstrapping and estimate the 90, 95, 99 and 99.9% confidence intervals. We report the correlation coefficient $\pm$ the standard deviation of the simulated values.

Results

Seed mass ranged from 0.08 (*G. mostii*) to 1.95 mg (*Harrisia pomanensis*) (Table 1). Seed mass and final germination percentage were not significantly related under light conditions ($r = -0.17 \pm 0.18$, $P \geq 0.1$; Fig. 1a). Seed mass and RLG were not related ($r = -0.05 \pm 0.29$, $P \geq 0.1$; Fig. 1b). Only two species (*Echinopsis aurea* and *Cereus hankeanus*) were classified

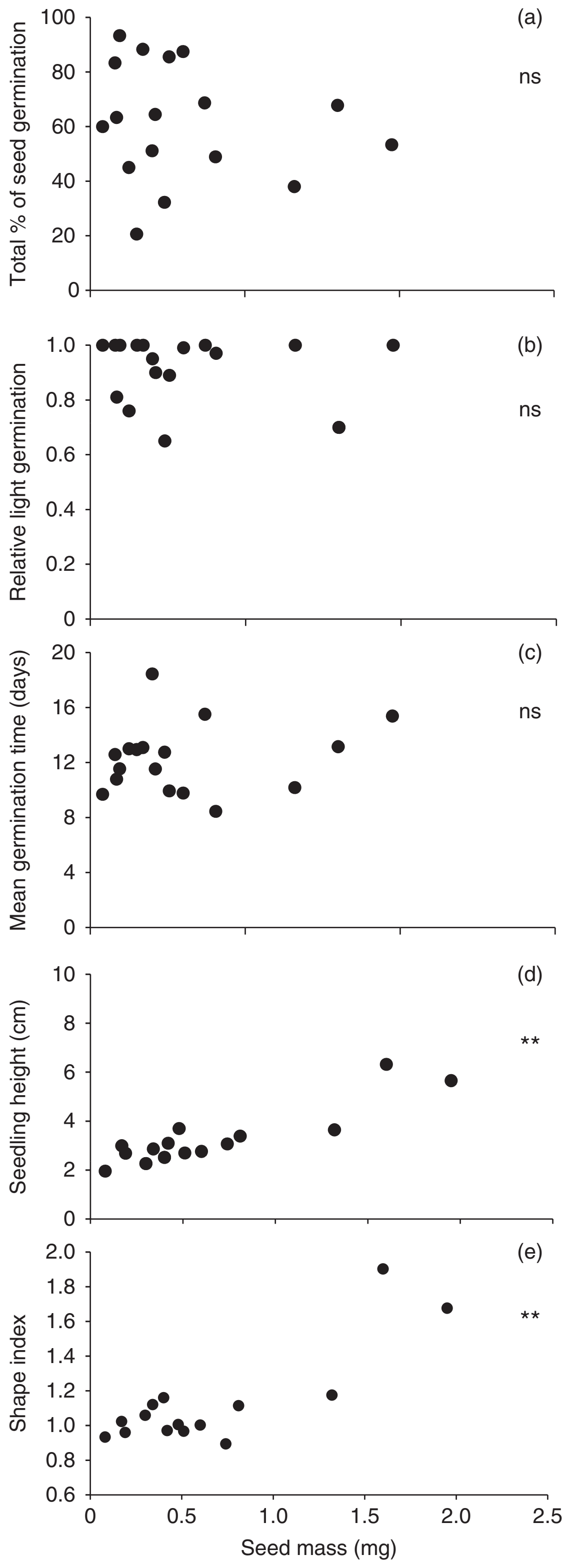

Figure 1. Relationships between seed mass and (a) total percentage of seed germination; (b) relative light germination (RLG); (c) mean germination time (MGT, days); (d) seedling height (mm); and (e) shape index in cacti species from central Argentina. **, $P \leq 0.001$; ns, non-significant; Pearson correlations.

as light indifferent, with the remaining species being positively photoblastic (Table 1). Eight species did not germinate in the darkness, whereas in this treatment the maximum germination achieved was 28.89% in *C. hankeanus* (Table 1). Seed mass and MGT were not significantly related either ($r = 0.17 \pm 0.24$, $P \geq 0.1$; Fig. 1c). All species started to germinate before the fifth day of the experiment.

Seedling width, height and volume were positively related to seed mass, with height being the measure that best correlated with seed mass ($r = 0.89 \pm 0.10$ $P \leq 0.001$; Fig. 1d). In addition, seedling shape was also related to seed mass ($r = 0.83 \pm 0.19$ $P \leq 0.05$; Fig. 1e). We found that 13 of the 15 species presented a shape index close to 1 (Fig. 1e), indicating that they are 'globose' seedlings. The other two species, *C. hankeanus* and *H. pomanensis*, presented values of 1.5 and 1.9, respectively, indicating that they are 'columnar seedlings'. Interestingly, all globose species (as adults) presented globose seedlings, but not all columnar species presented columnar seedlings. Particularly, seedlings of *Cleistocactus baumannii*, *Echinopsis leucantha* and *S. coryne* were globose.

Discussion

For cactus species from central Argentina, seed mass was not related to the total germination percentage. These results are in agreement with some studies performed in different plant species from wetlands, dry grasslands and forests (e.g., Shipley and Parent, 1991; Morgan, 1998; Chen *et al.*, 2002; Sautu *et al.*, 2006; Liu *et al.*, 2007). However, other studies also conducted in those ecosystems showed a significant relationship (positive and/or negative) between seed mass and total germination (e.g. Milberg *et al.*, 2000; Bu *et al.*, 2007; Galíndez *et al.*, 2009; Wang *et al.*, 2009). In agreement with the results found by Rojas Aréchiga *et al.* (2012) in cactus species, our results suggest that total percentage of seed germination could be related to factors other than seed mass (Paz *et al.*, 1999; Wang *et al.*, 2009).

We found no relationship between RLG and seed mass. Germination of almost all species was found to be light dependent, which is in agreement with previous studies in cactus species (Flores *et al.*, 2006; Gurvich *et al.*, 2008; Ortega-Baes *et al.*, 2010; Guerrero *et al.*, 2011; Rojas-Aréchiga *et al.*, 2012). By contrast, Flores *et al.* (2011) found a weak negative but significant relationship between seed mass and RLG; this difference may be due to the broader seed mass range used in that work (0.046–16 mg) than the range we used (0.087–1.958 mg).

MGT for all species ranged between 8.45 and 18.44 d; these values are similar to those reported for four taxa of the genus *Arthrocereus* (Cactaceae) from south-eastern Brazil (Cheib and García, 2012) and from previous studies in the present area (Gurvich *et al.*, 2008). In addition, these values are common for plants, even among contrasting growth forms (Norden *et al.*, 2009). Theoretical models predict that large-seeded species would germinate more rapidly than small ones. In this study seed mass was not related to MGT. All species germinated relatively quickly, independently of their mass, showing/suggesting that they do not have any type of dormancy, and that seed mass is not an important selection force that affects germination velocity.

Our results show that seed mass was only related to seedling size and shape. As expected, heavier-seeded species may produce bigger seedlings. This result is in accordance with previous studies that found a positive relationship between seed mass and seedling size for plants of other families (Leishman *et al.*, 2000). A large seed mass may provide large seed reserves, which may guarantee large seedling size and high tolerance to any stress factors (e.g. drought, shade; Leishman *et al.*, 2000; Bowers and Pierson, 2001; Baraloto *et al.*, 2005). We found a positive relationship between seed mass and shape index. Heavy seeds produce ‘columnar seedlings’. In our study, all globose species presented globose seedlings, but not all columnar species presented columnar seedlings. Particularly, seedlings of *E. leucantha*, *S. coryne* and *C. baumannii*, all columnar species, have globose seedlings. Columnar seedlings would be better competitors for light, but globose seedlings would be more resistant to temperature variations due to their lower surface/volume ratio. To our knowledge, no study has analysed seed mass in relation to seedling shape.

In conclusion, theory suggests that seed mass is a key variable for predicting patterns of plant regeneration (Leishman *et al.*, 2000; Daws *et al.*, 2008). Apparently, this pattern is most evident at the species level (van Mölken *et al.*, 2005). In Cactaceae the available data do not allow us to establish a general pattern in the relationship between seed mass and germination characteristics. In addition, the germination response observed could be a species-specific trait independent of seed mass. On the other hand, our results suggest that seed mass would directly affect seedling establishment, which is a key demographic process in cacti (Bowers and Pierson, 2001; Rojas-Sandoval and Meléndez-Ackerman, 2013). Our study also provides essential data about the regenerative biology of some species of this interesting plant group.

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Conflicts of interest

None.

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